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Relationships of Pocket Gophers of the Genus *Geomys* from the Central and Northern Great Plains

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and
Robert M. Timm

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Museum of Natural History

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Relationships of Pocket Gophers of the Genus *Geomys* from the Central and Northern Great Plains

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INTRODUCTION

Pocket gophers have received much attention recently as models of the processes of genic differentiation and speciation because of their low vagility and high degree of local morphological differentiation (e.g., Patton and Yang, 1977; Patton and Feder, 1978, 1981; Patton *et al.*, 1979; Patton and Smith, 1981; Thaeler, 1974). Evolutionary studies, such as those utilizing biochemical data, are based on the current taxonomy, which traditionally has been based on morphological studies. Unfortunately, the only comprehensive revision of Recent geomyids (Merriam, 1895), necessarily relied entirely on qualitative assessments of relationships of species and geographic variation within species, and has been outdated by numerous publications of more limited scope. Many of the studies on which the currently accepted taxonomy is based (see Hall, 1981) were restricted to small geographic areas, few taxa, and, all too often, small sample sizes.

In the course of studies of coevolution of pocket gophers of the genus *Geomys* and their lice (Timm, 1979), it became apparent that a comprehensive review of morphological variation and taxonomy of this genus, especially the widespread, diverse populations referred to the species *Geomys bursarius,* was much needed. We began such an investigation, and early in the study our attention focused on the northern and central portions of the area in which *G. bursarius* occurs, partly because of the obvious need for work, and partly because other studies were in progress in New Mexico, Oklahoma, and Texas (Baker and Genoways, 1975; Honeycutt and Schmidly, 1979; Tucker and Schmidly, 1981; Bohlin and Zimmerman, 1982). We have given special attention to the status of formerly recognized species that have more recently been relegated to subspecific status. We have not dealt with *Geomys pinetis* from the southeastern United States, or with the *G. arenarius*/*G. personatus* group from Texas and adjacent areas.

History of Taxonomic Investigations

The first species of pocket gopher to be named in the Linnaean system was *Mus bursarius* Shaw, 1800, from "the interior of Canada." *Mus tuza* Ord, 1815, from the pine barrens near Augusta, Georgia, was the next species named; this name is now rejected as a *nomen dubium* (see Harper, 1952), but is an equivalent of *Geomys pinetis.* In 1817 Rafinesque described several new species of pocket gophers, proposed new names for the previously described species, and erected two new genera, *Geomys* and *Diplostoma.* Because the two species included in *Diplostoma* are now known to be junior synonyms of *Mus bursarius,* which Rafinesque included in the genus *Geomys, Diplostoma* is now considered to be a junior synonym of *Geomys.* Although some controversy remains over the species to which the name *Mus bursarius* was applied (see Merriam, 1895), current usage and relative certainty about the proper allocation of the name suggest that the name *bursarius* should continue to be applied as it has been since the mid-1800's.

The next valid genus to be proposed was *Thomomys* Wied-Neuwied, 1839, although several genera were proposed in the interim which are now considered to be synonyms of *Geomys.* Subsequent to 1839 and prior to 1895, gophers with grooved incisors were referred to *Geomys* or one of its synonyms, and gophers with ungrooved incisors were referred to *Thomomys.* Merriam (1895) named several new genera of gophers based on species previously assigned to *Geomys.* Although these genera have undergone taxonomic changes (Russell, 1968), the generic status of *Geomys* has been stable since that time. The following comments refer only to those taxa included in *Geomys* as currently defined.

Geomys breviceps was named by

Baird in 1855 on the basis of specimens from Louisiana; he referred specimens from Louisiana, Texas, and Kansas to *breviceps,* whereas specimens of this genus from the northern portions of the Great Plains (Illinois, Kansas, Minnesota, Missouri, Nebraska, and Wisconsin) were assigned to *G. bursarius.* No other taxa were named until Merriam began his studies of the genus, naming *G. bursarius lutescens* from central Nebraska in 1890, and *G. breviceps attwateri, sagittalis,* and *texensis* (all from Texas) in 1895. In Merriam's (1895) revision of the genus, he reassigned a number of taxa, and recognized three species groups. One of these, the *tuza* (=*pinetis*) group, does not concern us here. The *G. bursarius* group was monotypic as he defined it; he noted a variety of features distinguishing it from the other groups, including an elongate and angular skull, high sagittal crest, and palatine bones with ascending wings broadly articulated with the horizontal shelf of the orbitosphenoids. Finally, the *texensis–breviceps* group included five species: *arenarius, breviceps, lutescens, personatus,* and *texensis.* He considered all five to be closely related, and probably much like the stock that gave rise to the *G. tuza* (=*pinetis*) and *G. bursarius* groups. Merriam considered the species *G. lutescens,* occurring from Oklahoma north to South Dakota and Wyoming, to be the closest relative of *G. breviceps.* This classification was accepted for over half a century, although between 1895 and 1947, fourteen additional taxa were described, all as subspecies of either *G. breviceps* (*llanensis, brazensis, ammophilus, dutcheri, ludemani, major, pratincolus,* and *terricolus*), *G. bursarius* (*illinoensis* and *majusculus*), or *G. lutescens* (*hylaeus, jugossicularis, levisagittalis,* and *vinaceus*).

Beginning in 1947 taxonomic changes were made which involved *G. breviceps, bursarius, lutescens,* and *texensis.* The following discussion deals only with these species: i.e., it excludes *G. arenarius* and *personatus.*

Villa-R. and Hall (1947) stated that they had evidence of intergradation between all taxa that occurred in Kansas, and so considered them to represent a single species, *G. bursarius.* At the same time, they described a new subspecies, *G. b. industrius.* Because subspecies of *bursarius, lutescens,* and *breviceps* as then defined occurred in Kansas, they implied that all taxa previously included in these species were conspecific, and Baker and Glass (1951) formally synonomized *G. breviceps* with *G. bursarius* on the basis of putative evidence of intergradation between the taxa *G. breviceps dutcheri* and *G. bursarius major* in Oklahoma.

Subsequently, three additional forms have been described as subspecies of *G. bursarius* (*wisconsinensis, missouriensis,* and *knoxjonesi*). Russell and Jones (1956) considered the subspecies *G. b. vinaceus* to be a synonym of *G. b. lutescens,* and Jones (1964) also synonomized *G. b. hylaeus* and *G. b. levisagittalis* with *G. b. lutescens.* Lowery (1974) considered *G. b. pratincolus* to be a synonym of *G. b. dutcheri.* In the latter three cases, the small degree of difference between surrounding populations, and the high degree of morphological variability (both within and between populations) were cited as the basis for the changes.

Honeycutt and Schmidly (1979) recently investigated the relationships of those members of the *G. bursarius* complex found in Texas. They synonomized *brazensis, dutcheri, ludemani, pratincolus,* and *terricolus* with *G. b. sagittalis,* and *ammophilus* with *G. b. attwateri.* They also noted the presence of three groups of subspecies which they suspected of acting as independent species; however, they did not elevate them to species rank. The groups were the *lutescens* group (including *lutescens, major, knoxjonesi, llanensis,* and *texensis*), the *attwateri* group (including only *attwateri*), and the *breviceps* group (including *breviceps* and *sagittalis*). Tucker and Schmidly (1981) have subsequently

shown that *attwateri* does not intergrade with the *G. breviceps* group, and recommended that it be recognized as a valid species. Bohlin and Zimmerman (1982) detected no electrophoretic evidence of intergradation between *breviceps* and *major* in Oklahoma, and elevated *G. breviceps* to species status.

As a consequence of our studies, which are described in detail below, we became convinced that the current taxonomy does not reflect the actual number of species in the *Geomys bursarius* complex. As is demonstrated below, the presumed evidence for intergradation between *G. bursarius* and *G. lutescens* was misinterpreted or in error. We feel that the data presented by Honeycutt and Schmidly (1979) are sufficient to support the separation of *G. lutescens* and *G. breviceps,* and their results are strongly supported by recent investigations by Bohlin and Zimmerman (1982). Therefore, for the reasons discussed below, we recognize four species of pocket gophers in the *Geomys bursarius* species group in the Great Plains, *G. attwateri, G. breviceps, G. bursarius,* and *G. lutescens.*

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METHODS AND MATERIALS

The fundamental question addressed in this study was, how many species of *Geomys* exist in the central United States north of Texas? We approached the problem by grouping individuals into operational taxonomic units (OTUs), with each OTU consisting of gophers from a very limited, ecologically homogeneous area, usually one to three counties. Means from the OTUs were used to describe geographic variation in size. The OTUs were then subjected to principal components and cluster analyses based on external and cranial measurements and one qualitative cranial character in order to describe geographic patterns of similarity. We then tested the null hypothesis of no difference between adjacent populations by a series of discriminant function analyses. These tests for significant differences are most meaningful when taken in the context of a geographically large area and many populations; thus, we considered approximately one-fourth of the OTUs simultaneously in each of four analyses as described below. We included at least 20 OTUs from three states in each analysis, including some OTUs also used in preceding or following analyses, in order to simplify comparison of results.

Discriminant function analysis was used in this study in two different contexts, and both deserve comment. The first use was as a means of comparing populations, i.e., testing the null hypothesis of no difference between populations. Discriminant function analysis is designed to maximize intergroup variance and minimize intragroup variance; it is

most often used as a method of assigning individuals (cases) into predetermined groups (usually two groups). Because discriminant function analysis is a powerful discriminator, spurious results may be obtained if the predetermined groups are not defined correctly. For example, two small (n less than 50) samples drawn from a single population may be significantly discriminated in many cases because of random differences due to sampling error. However, the significance levels drop with the addition of more individuals and/or groups. Experimentation has shown us that addition of an "outgroup," i.e., a population known to be different, usually will cause spurious discrimination to drop below the level of statistical significance, and for classification functions to show great overlap between spurious or artificial groupings. The results described below show that, when samples of pocket gophers drawn from broad geographic areas are analyzed simultaneously, many groups are not distinguishable, in spite of the strong discriminatory power of the algorithm. However, some groups are easily distinguished at high significance levels, demonstrating that the discriminatory power of the algorithm does not break down when large numbers of groups (up to 20) are considered simultaneously. Thus, one can test the hypothesis of distinctness of each and all populations of a taxonomic unit. Use of the discriminant function analysis has the advantage of allowing multivariate comparison of identified groups (populations) rather than individuals; this capacity is not available in other analyses. Definition of OTUs from small, ecologically homogeneous habitats minimizes the likelihood of mistakenly including individuals from two different taxa, but the possibility for such an error does remain, and can be dealt with most effectively by careful screening of OTUs by the investigator.

The second use of discriminant function analysis in this study was as a means of detecting intermediacy of individuals between two previously determined parental populations. Neff and Smith (1979) have demonstrated that known hybrid fish are often not correctly identifiable as hybrids using this technique; however, they note that the presence of at least some hybrid individuals is always detectable using this method if moderately large samples are available. We have used the analysis in a way consistent with their results; i.e., we have used the method only to detect the presence of hybridization on a broad scale, not to identify individuals as F_1s, F_2s, etc., and have been conservative in drawing conclusions. However, we point out that one may not assume that hybrid mammals characteristically show a tendency to resemble one or the other parental type simply because fish do so, especially since some limited evidence argues against this (see examples of mammalian hybrids discussed by Gray, 1972). This could be investigated either by raising hybrids in a laboratory setting (as Neff and Smith did), or by determining the correlation between morphological intermediacy (such as that graphed in Fig. 11) and an independent measure of genetic intermediacy, such as an allelic intermediacy value derived from genetic studies.

Approximately 1,400 adult pocket gophers were examined. Males and females were analyzed separately; only adults were included in analyses. Adults were defined as those individuals which had the basioccipital suture fused completely, and those individuals which had cranial crests strongly developed but which had the basioccipital suture only partly fused. Unless stated otherwise, all comments below refer to adult females. Our samples of females were larger than those of males, and females showed less growth of the cranial crests after suture fusion; for these reasons we feel that female gophers are in general more appropriate for use in multivariate statistical analyses for taxonomic purposes.

Cranial measurements were taken by

Heaney with dial calipers graduated to 1/20 mm; these measurements were taken as defined in DeBlase and Martin (1974), except for the following. Length and width measurements were taken of that portion of the frontals which projects between the premaxillaries on the dorsal surface of the skull; this part of the frontal is referred to here as the "frontal square." Orbital length was taken from the anteriormost point in the orbit to the most posterior point in the "orbit" (the orbit is confluent with, and for convenience is here regarded as including, the temporal fossa). "Maxillary visibility" was taken as 0.0, 0.5, or 1.0, based on whether the sides of the rostrum were visible over the edge of the rostrum at the notch anterior to the zygomatic arches on both sides (1.0), or were obscured by a horizontal projection of the premaxillary on both sides (0.0), or one side only (0.5). External measurements were taken from specimen labels. Bacula were measured by Heaney to the nearest 0.01 mm using a craniometer.

We grouped 665 adult females into 80 OTUs and 258 adult males into 40 OTUs. OTUs consisted of all adults available for study from a given county, group of adjacent counties, or part of a county, as defined in the following list. OTU numbers in tables 1 and 2 and Fig. 4 refer to these county groupings: 1. Kansas: Morton and Stanton. 2. Kansas: Seward. 3. Kansas: Gray. 4. Kansas: Meade. 5. Kansas: Clark. 6. Kansas: Comanche, Edwards, and Kiowa. 7. Kansas: Barber. 8. Kansas: Harper. 9. Kansas: Cowley. 10. Kansas: Hamilton. 11. Kansas: Kearny. 12. Kansas: Finney. 13. Kansas: Ford. 14. Kansas: Cheyenne and Sherman. 15. Kansas: Rawlins and Thomas. 16. Kansas: Decatur and Norton. 17. Kansas: Graham. 18. Kansas: Rooks. 19. Kansas: Greeley, Logan, Wallace, and Wichita. 20. Kansas: Trego. 21. Kansas: Ellis. 22. Colorado: Adams and Morgan. 23. Colorado: Larimer, Logan, and Weld. 24. Colorado: Boulder and Douglas. 25. Wyoming: Converse, Niobrara, and Weston. 26. Wyoming: Goshen, Laramie, and Platte. 27. Nebraska: Scotts Bluff. 28. Nebraska: Banner, Cheyenne, and Kimball. 29. Nebraska: Sioux. 30. Nebraska: Dawes and South Dakota: Fall River. 31. South Dakota: Bennett, Jackson, Todd, and Washabaugh. 32. Nebraska: Boyd and Keya Paha. 33. Nebraska: Brown, Cherry, and Rock. 34. Nebraska: Holt. 35. Nebraska: Lincoln. 36. Nebraska: Buffalo, Custer, Dawson, and Valley. 37. Nebraska: Dundy and Hitchcock. 38. Nebraska: Harlan and Kearney. 39. Nebraska: Franklin. 40. Nebraska: Antelope (western edge). 41. Nebraska: Antelope (from western edge of hybrid zone described by Heaney, 1979). 42. Nebraska: Antelope (hybrids). 43. Kansas: Greenwood. 44. Kansas: Mitchell. 45. Kansas: Cloud and Republic. 46. Kansas: Riley. 47. Kansas: Marshall. 48. Kansas: Douglas. 49. Missouri: St. Charles and St. Louis. 50. Nebraska: Butler, Gage, and Lancaster. 51. Nebraska: Antelope (central, from eastern edge of hybrid zone described by Heaney, 1979). 52. Nebraska: Knox and Platte. 53. Missouri: Atchison, Buchanan, and Clay. 54. Iowa: Des Moines and Missouri: Clark, Marion, and Scotland. 55. Iowa: Mahaska, Marshall, Monroe, and Story. 56. Iowa: Clayton and Dubuque. 57. Iowa: Clay and Emmett and Minnesota: Brown. 58. Minnesota: Goodhue, Houston, and Winona. 59. Minnesota: Ramsey and Sherburne. 60. Minnesota: Becker, Cass, Kittson, Norman, and Polk. 61. South Dakota: Brookings, Lake, and Moody and Minnesota: Rock. 62. South Dakota: Grant and Minnesota: Traverse. 63. North Dakota: Richland. 64. North Dakota: Cass, Grand Forks, La Moure, and Trail. 65. Wisconsin: Bayfield, Burnett, and Douglas. 66. Wisconsin: Crawford and Richland. 67. Illinois: DeWitt, Logan, Mason, and McLean. 68. Illinois: LaSalle, Marshall, Tazewell, and Woodford. 69. Illinois: Cass, Madison, Mason, Morgan, and St. Clair. 70. Illinois: Kankakee and Will and Indiana: Jasper, Newton, and Tippecanoe. 71. Oklahoma:

TABLE 1.—Means (± standard deviation) for adult females for each of the OTUs utilized in this study.

OTU#	N	Total Length	Tail	Hind foot	Condylobasal Length	Zygomatic Breadth	Mastoid Breadth	Nasal Breadth	Frontal Square Length	Frontal Square Breadth	Orbital Length	Maxillary Visibility
1	7	239.0±10.3	73.3±06.1	30.4±1.5	41.86±1.29	25.93±0.84	25.03±0.84	8.93±0.27	4.36±0.48	1.47±0.29	14.70±0.62	1.0±0.0
2	4	235.7±07.8	70.3±05.1	29.5±1.7	41.60±0.82	26.23±0.30	24.83±0.25	9.35±0.44	4.30±0.42	1.58±0.17	14.78±0.43	1.0±0.0
3	9	243.8±11.5	73.9±06.6	31.1±1.5	41.52±0.64	25.87±0.96	24.56±0.71	8.44±0.14	4.23±0.41	1.70±0.34	14.26±0.36	1.0±0.0
4	9	239.3±10.9	73.4±05.2	31.2±1.6	41.80±1.14	25.81±0.73	24.48±0.78	9.10±0.22	4.18±0.61	1.71±0.31	14.63±0.54	0.9±0.3
5	6	241.2±05.7	70.7±04.7	30.8±0.8	42.23±0.96	26.58±1.14	25.17±1.22	9.45±0.36	3.97±0.68	1.60±0.38	14.85±0.56	0.8±0.4
6	8	229.6±12.9	70.4±05.3	31.0±2.6	42.19±1.71	26.45±1.35	24.50±1.24	9.16±0.50	3.85±0.52	1.51±0.21	14.75±0.59	0.8±0.5
7	22	237.0±14.4	71.3±08.6	29.9±1.7	42.11±1.41	26.21±0.71	24.52±0.94	9.12±0.33	3.72±0.49	1.55±0.33	14.35±0.63	1.0±0.2
8	4	246.0±21.5	66.8±11.0	29.3±0.5	42.15±1.22	26.28±1.26	23.90±0.47	9.65±0.42	3.35±0.64	1.93±0.30	14.45±0.62	0.3±0.5
9	3	238.0±03.5	68.7±02.5	30.7±0.6	42.40±1.77	26.77±1.55	24.73±1.21	9.20±0.53	4.40±0.66	1.03±0.12	15.20±0.44	1.0±0.0
10	4	242.0±10.7	71.5±04.4	29.8±1.0	42.15±1.07	26.50±1.33	24.98±0.68	9.00±0.27	4.30±0.48	1.53±0.19	14.43±1.01	0.6±0.5
11	6	246.0±10.4	71.0±06.0	30.5±1.9	42.75±1.44	26.60±0.41	24.53±0.69	9.36±0.66	3.58±0.57	1.60±0.39	14.62±0.76	0.3±0.3
12	5	237.0±07.6	68.6±02.2	30.0±0.7	40.44±0.98	24.80±0.65	23.80±1.15	9.04±0.23	3.90±0.69	1.62±0.36	14.04±0.50	0.7±0.5
13	5	231.0±10.7	67.4±08.0	30.4±2.2	42.26±1.78	26.12±0.82	24.66±0.70	9.14±0.36	4.14±0.23	1.44±0.46	14.78±0.58	1.0±0.0
14	14	243.0±12.9	74.5±06.2	30.4±0.9	42.93±1.46	26.58±1.09	24.16±0.63	9.51±0.45	3.14±0.36	1.86±0.33	14.65±0.68	0.2±0.4
15	10	238.8±07.6	67.4±04.9	29.1±1.5	41.87±0.63	25.90±0.39	24.02±0.35	9.46±0.54	3.08±0.45	1.90±0.43	14.10±0.33	0.3±0.5
16	7	240.7±11.2	70.9±10.9	32.4±3.8	41.94±1.26	26.11±1.10	23.71±0.88	9.37±0.31	2.73±0.45	2.01±0.34	14.59±0.78	0.6±0.5
17	12	244.6±08.1	73.1±06.0	31.4±1.6	43.62±0.96	27.59±0.75	24.75±0.92	10.43±0.51	3.05±0.41	1.81±0.26	14.55±0.49	0.1±0.3
18	10	247.3±07.1	73.7±05.4	31.1±1.0	43.24±0.81	26.95±0.72	24.26±0.41	10.44±0.48	3.27±0.41	1.80±0.16	14.37±0.42	0.0±0.0
19	7	233.4±15.7	70.0±08.2	30.4±1.6	40.93±1.07	24.86±0.62	23.16±0.85	9.10±0.42	3.13±0.49	1.83±0.16	14.29±0.41	0.4±0.5
20	9	241.0±04.2	71.7±06.3	29.3±1.8	42.00±1.28	26.40±1.06	23.77±1.17	9.56±0.55	3.20±0.48	1.90±0.25	14.24±0.58	0.2±0.4
21	21	241.0±10.3	70.2±04.9	29.7±1.5	41.86±1.06	26.39±1.05	23.94±0.70	9.55±0.42	2.93±0.43	1.84±0.28	13.95±0.37	0.1±0.2
22	23	241.0±08.5	76.6±05.1	31.0±1.1	42.18±0.97	26.29±0.88	24.00±0.67	9.93±0.64	3.61±0.37	1.37±0.22	14.31±0.44	0.2±0.4
23	18	237.3±12.5	66.7±07.3	30.7±1.7	41.89±0.99	26.71±0.88	23.59±0.62	9.33±0.38	3.65±0.42	1.46±0.36	14.00±0.31	0.6±0.5
24	5	234.0±07.2	64.2±06.8	29.6±2.5	41.06±1.68	25.84±0.74	23.62±0.86	9.28±0.29	3.72±0.19	1.60±0.44	14.12±0.57	0.4±0.6
25	13	243.2±09.5	70.3±05.0	31.6±1.5	41.89±1.50	25.59±0.73	23.90±0.99	9.51±0.36	3.68±0.49	1.65±0.54	14.25±0.55	1.0±0.0
26	6	245.3±10.2	75.5±07.5	31.8±0.4	42.58±1.40	26.85±1.30	24.63±0.63	9.40±0.34	3.55±0.58	1.80±0.27	14.32±0.84	0.8±0.4
27	5	240.0±04.5	70.2±04.1	31.2±0.8	41.28±0.94	25.92±0.79	24.20±0.46	9.24±0.40	3.40±0.46	1.70±0.37	14.30±0.48	0.8±0.5
28	8	235.9±11.0	65.6±06.3	30.5±1.1	40.34±1.09	25.04±0.95	23.04±0.69	9.18±0.43	3.21±0.65	1.61±0.25	13.88±0.51	0.5±0.5
29	5	252.6±12.0	70.8±09.0	31.4±1.5	42.98±1.30	27.28±0.54	25.40±0.95	9.66±0.46	3.96±0.46	1.70±0.31	14.70±0.50	0.6±0.6
30	35	239.5±10.0	66.6±05.6	30.6±1.5	41.87±1.14	26.44±0.96	24.52±0.81	9.65±0.41	3.95±0.50	1.91±0.43	14.26±0.51	0.6±0.5
31	5	244.6±14.9	71.8±07.5	32.6±1.7	43.30±1.36	27.14±1.49	24.60±1.28	9.50±0.20	3.30±0.46	1.38±0.58	14.90±0.53	0.7±0.4
32	8	248.3±10.9	71.3±04 6	30.4±1.2	43.15±0 63	27.44±0 89	25 09±0.72	9.61±0.33	3.46±0.47	1.89±0.29	15.10±0.41	0.8±0.4
33	5	231.0±06.0	62.4±05.1	30.4±0.9	41.36±0.76	25.80±0.42	23.64±0.63	9.68±0.19	3.62±0.63	1.64±0.35	14.26±0.18	0.2±0.3
34	6	246.5±11.5	71.8±09.8	31.1±1.6	43.30±0.81	27.20±0.61	24.53±0.41	9.77±0.40	3.67±0.45	1.70±0.28	14.95±0.55	0.3±0.5
35	18	232.7±13.3	65.2±09.2	30.2±1.9	41.76±1.94	25.89±1.32	24.10±1.23	9.36±0.52	3.85±0.59	1.60±0.60	14.19±0.84	0.6±0.4
36	7	227.9±22.1	64.3±07.3	29.9±2.0	42.23±0.88	26.39±0.70	24.23±0.89	9.40±0.33	3.94±0.53	1.61±0.31	14.40±0.47	0.8±0.4
37	6	238.0±11.4	69.8±05.2	30.5±1.9	41.57±1.26	25.88±1.09	23.82±0.74	9.20±0.51	3.52±0.28	1.32±0.19	14.00±0.49	0.4±0.5
38	5	218.8±12.9	56.6±07.9	28.8±1.5	39.42±1.10	24.60±0.59	22.66±0.98	8.94±0.71	3.42±0.40	1.86±0.58	13.70±0.23	0.3±0.5

39	6	224.5±18.1	59.2±09.5	29.5±2.2	40.03±1.80	24.87±0.84	22.80±0.94	9.08±0.72	3.43±0.36	1.82±0.53	13.70±0.21	0.3±0.4
40	10	246.2±12.6	74.3±06.8	28.8±1.9	42.02±1.00	26.50±0.54	24.25±0.71	9.76±0.33	4.08±0.43	1.98±0.39	14.48±0.49	0.2±0.4
41[1]	8	238.6±11.1	74.8±08.1	29.9±0.8	41.00±1.08	25.43±1.05	23.44±0.87	9.16±0.37	3.66±0.42	1.46±0.47	14.15±0.52	0.6±0.5
42	14	249.5±07.4	74.1±05.8	30.9±0.9	43.06±0.87	26.89±1.04	24.76±0.75	9.55±0.37	3.92±0.39	1.56±0.43	14.94±0.35	0.6±0.5
43	10	263.8±11.7	77.0±05.3	31.9±1.9	45.00±0.96	27.71±0.84	25.49±0.53	9.24±0.24	3.99±0.66	1.60±0.24	15.49±0.62	0.8±0.4
44	6	268.2±05.9	74.7±06.1	32.7±1.0	47.10±1.05	29.16±0.93	27.42±0.56	9.57±0.44	3.93±0.45	1.90±0.17	15.65±0.43	0.7±0.5
45	9	262.8±08.7	80.7±07.0	33.8±1.6	47.71±1.06	29.01±0.85	27.19±0.62	10.02±0.25	4.20±0.85	1.72±0.35	15.93±0.73	1.0±0.0
46	6	263.5±05.2	76.7±03.1	32.8±1.6	46.70±0.91	29.13±0.92	26.75±0.67	9.83±0.48	3.62±0.46	1.80±0.34	16.08±0.52	0.3±0.5
47	6	273.5±10.5	80.8±05.8	33.7±2.3	47.92±1.38	28.77±0.77	27.02±0.78	9.70±0.26	3.78±0.84	1.93±0.10	16.28±0.60	1.0±0.0
48	14	261.6±11.3	75.0±06.8	33.6±2.7	46.79±1.42	28.30±0.66	26.26±1.18	9.85±0.30	3.72±0.71	1.98±0.30	15.50±0.53	0.4±0.5
49	7	264.6±11.1	72.4±03.5	31.3±1.0	46.40±1.15	28.70±1.04	25.94±1.27	9.65±0.28	3.73±0.51	1.74±0.41	15.69±0.51	0.7±0.5
50	21	277.5±11.0	75.1±06.5	34.9±1.7	49.04±1.49	29.83±0.99	27.96±1.28	10.23±0.45	3.68±0.37	2.02±0.35	16.14±0.68	0.9±0.4
51[2]	8	274.1±10.0	78.9±04.6	34.3±1.3	47.23±1.09	30.04±1.27	27.75±0.71	9.93±0.44	3.93±0.63	2.06±0.23	15.99±0.53	0.7±0.5
52	4	264.3±09.8	75.0±04.7	34.0±1.4	46.03±0.82	27.68±1.56	25.80±0.84	10.20±0.18	3.45±0.17	2.18±0.33	15.23±0.83	0.9±0.3
53	4	279.3±11.2	81.0±16.3	34.8±1.3	48.00±2.04	29.43±1.48	26.98±0.98	9.93±0.22	3.65±1.26	2.08±0.35	15.65±0.84	0.8±0.5
54	5	254.2±16.4	70.2±08.9	32.8±2.2	45.90±2.25	28.90±1.71	25.96±1.17	9.76±0.57	3.94±0.23	1.82±0.65	15.76±0.93	0.8±0.4
55	3	289.0±05.2	80.0±03.6	33.6±0.6	50.67±0.96	29.70±0.60	28.73±0.84	10.00±0.10	4.23±0.11	2.20±0.20	17.23±0.81	1.0±0.0
56	8	285.8±09.1	75.6±15.3	31.1±1.4	50.53±1.44	30.60±1.10	28.56±0.90	10.18±0.18	3.93±0.77	2.28±0.35	16.56±0.79	0.6±0.5
57	3	264.0±28.8	73.3±15.9	34.0±1.7	48.83±2.16	28.70±1.57	26.87±1.11	9.80±0.10	3.97±0.50	1.90±0.36	15.87±1.19	1.0±0.0
58	4	267.8±27.5	67.8±10.6	32.8±1.7	46.93±1.67	28.40±1.51	26.63±1.33	9.45±0.48	3.95±0.26	2.10±0.29	16.18±0.87	1.0±0.0
59	14	262.1±13.5	66.9±07.3	33.3±1.3	47.08±1.46	28.09±0.90	25.75±0.90	9.66±0.33	3.87±0.46	1.89±0.33	16.04±1.00	0.9±0.3
60	7	246.7±27.9	72.0±07.3	33.3±1.5	46.74±1.73	27.54±0.95	25.70±1.15	9.64±0.40	4.01±0.90	1.91±0.37	15.76±0.79	1.0±0.0
61	11	274.8±09.6	73.6±04.4	35.2±1.4	49.33±0.86	29.92±0.89	27.77±0.93	10.04±0.32	4.47±0.48	2.36±0.26	16.32±0.53	1.0±0.0
62	4	267.5±05.3	72.3±09.5	35.8±1.5	49.45±1.59	29.35±0.93	27.40±0.91	9.95±0.39	3.83±0.43	2.23±0.28	16.40±1.05	1.0±0.0
63	5	268.0±11.6	77.4±05.1	35.4±0.9	47.10±0.74	28.68±0.49	26.24±0.57	10.18±0.34	3.80±0.68	2.12±0.36	15.74±0.37	0.2±0.3
64	6	270.5±15.8	75.0±07.7	34.8±1.7	48.50±1.58	28.60±0.85	26.30±1.19	9.97±0.39	4.48±0.71	1.95±0.37	16.22±0.39	0.6±0.5
65	9	243.7±09.1	73.2±04.4	31.1±1.3	44.37±1.13	26.17±0.91	24.56±0.89	9.14±0.34	3.50±0.20	1.96±0.28	14.86±0.73	0.6±0.5
66	11	269.3±13.4	81.3±06.5	33.3±1.3	47.11±1.53	28.32±0.79	25.84±0.79	9.51±0.19	3.13±0.29	2.78±0.34	15.34±0.60	0.6±0.5
67	22	265.2±16.1	81.6±06.2	32.7±1.3	48.24±1.16	29.72±2.02	27.48±0.82	9.86±0.25	5.52±0.49	2.03±0.26	16.17±0.37	0.8±0.4
68	9	267.3±15.7	78.3±09.3	32.0±3.7	48.93±1.08	30.27±1.06	27.70±0.85	9.98±0.24	5.59±0.74	2.02±0.17	16.08±0.48	1.0±0.0
69	3	276.3±06.4	80.0±07.8	32.3±1.2	47.87±2.46	28.80±1.30	27.00±1.39	9.77±0.23	4.80±0.72	1.23±0.30	16.00±0.44	1.0±0.0
70	8	277.4±12.3	84.8±08.0	32.1±0.6	48.23±1.36	30.01±1.02	27.15±0.81	10.15±0.33	5.53±0.43	2.24±0.29	15.79±0.43	0.7±0.5
71	3	238.7±11.9	68.7±06.7	30.7±0.6	41.63±1.27	26.27±0.96	25.20±0.92	9.13±0.25	3.60±0.40	1.53±0.21	14.70±0.36	1.0±0.0
72	9	240.3±09.9	69.7±08.5	31.9±1.1	42.66±0.78	26.24±1.03	24.70±0.74	9.27±0.20	3.49±0.71	1.70±0.24	14.89±0.41	0.8±0.4
73	6	235.2±14.6	71.8±07.7	30.5±1.0	42.78±2.73	26.12±1.85	24.87±1.42	9.43±0.41	3.48±0.59	1.53±0.22	14.38±0.86	0.5±0.5
74	4	232.3±02.2	69.8±05.2	29.8±1.0	41.86±0.80	26.38±0.75	24.60±0.34	9.08±0.15	3.68±0.24	1.60±0.43	14.40±0.42	0.4±0.5
75	5	234.0±08.4	73.0±04.7	30.6±1.7	41.36±0.82	25.80±0.99	24.38±0.81	9.16±0.35	3.52±0.97	1.54±0.47	14.84±0.57	1.0±0.0
76	4	235.8±12.0	66.8±11.0	26.8±5.0	41.28±1.74	26.05±2.67	24.80±2.07	9.03±0.57	3.58±1.08	1.38±0.33	14.58±0.40	0.8±0.5
77	5	249.0±13.9	82.4±08.1	30.4±1.3	42.76±1.42	27.06±1.44	25.04±0.93	9.22±0.36	3.96±0.29	1.92±0.41	14.94±0.58	0.4±0.5
78	4	215.4±12.3	61.5±04.5	27.8±1.0	40.18±1.92	24.73±1.24	22.65±0.71	8.80±0.57	3.15±1.13	1.48±0.38	13.65±0.62	0.5±0.6
79	8	211.6±09.1	61.6±05.4	25.8±2.9	39.36±1.48	24.58±0.81	22.64±0.73	8.45±0.29	2.30±0.50	1.43±0.30	13.58±0.89	0.3±0.5
80	11	217.2±08.7	71.9±06.0	26.9±1.0	39.50±0.94	24.93±0.82	22.85±0.54	8.79±0.28	2.73±0.48	1.25±0.40	13.63±0.42	0.2±0.3

[1] From western edge of hybrid zone (Heaney, 1979).
[2] From eastern edge of hybrid zone (Heaney, 1979).

Cimarron and Texas. 72. Oklahoma: Beaver and Harper. 73. Oklahoma: Alfalfa and Woods. 74. Oklahoma: Major and Woodward. 75. Oklahoma: Custer, Dewey, and Ellis. 76. Oklahoma: Beckham, Caddo, and Washita. 77. Oklahoma: Harmon, Jackson, and Tillman. 78. Oklahoma: Adair, McIntosh, Muskogee, and Okfuskee. 79. Oklahoma: Atoka, Choctaw, Coal, and Pittsburg. 80. Oklahoma: Bryan and Marshall. 81. Kansas: Atchison and Leavenworth.

Multivariate analyses were conducted using programs in the BMDP series (Dixon, 1975) and MIDAS, the University of Michigan data analysis system; those used were the cluster (MIDAS CLUSTER); principal components analysis (MIDAS PRINCOM); and stepwise discriminant function analysis (BMDP7M). Cluster analysis was conducted using data generated by the principal components analysis. Data entered for each OTU were the scores on the first seven axes. Because the subsequent axes were not statistically significant, and accounted for less than 2% of the total variation, they would not have added meaningful information to the cluster analysis. This method limits the importance of size to 1/n of the total "characters," where n = number of axes. Use of unmodified data can allow size to play an excessive role in clustering. The cluster method used was an unweighted pair-group sum of squares utilizing the variance-covariance matrix. The cluster analysis of OTUs was used as a basis for detecting geographic patterns of similarity (Fig. 4). To construct this figure, the cluster phenogram (which had amalgamation distances of 0.412 to 36.361) was examined for identifiable geographic groupings at amalgamation levels of 5.0, 10.0, 15.0, 20.0, 25.0, and 30.0. Below the 10.0 level most groupings did not involve geographic neighbors, but at 10.0 a geographic pattern was evident; this is indicated on Fig. 4 by the inner (thinnest) line. Level 15.0 indicated further major groupings, and is shown as the middle line. Level 20.0 is the outer (heaviest) line in Fig. 4. Level 25.0 simply grouped OTU 66 to its neighbors, and so is not shown.

Discriminant function analyses used a tolerance level of .01; an F-to-enter of 1.0 rather than 4.0 was used as a stopping criterion because at 4.0 only one or two variables entered the model, and these primarily reflected size. An F-to-enter of 1.0 should maximize the ability to distinguish groups, and is thus consistent with our use of this analysis to test the null hypothesis of no difference between groups. Discriminant function analyses were conducted on several levels. An initial analysis was done on all OTUs having five or more specimens. This was done in four parts because of program and computer limitations; the four geographic units are defined in detail below. The second level of discriminant analysis consisted of lumping all OTUs which could not be significantly distinguished from one another (as indicated by non-significant F levels and jackknife classification levels of less than 90%). OTUs with samples smaller than five, and all specimens which had been noted in previous studies as potential intergrades, were entered as "unknowns." These unknowns were then assigned to taxa based on examination of posterior probabilities and plots of discriminant scores. The final level of analysis consisted of grouping together all individuals of each taxon, in order to ascertain the characters which are useful in identifying the taxa. The means of these taxa were used in producing a final phenogram of taxa (Fig. 10) using scores from a principal components analysis, as discussed above.

Specimens examined were housed in the following institutions:

American Museum of Natural History (AMNH)
Bemidji State University (BSU)
Chadron State College (CSC)
Colorado State University (CSU)
University of Colorado Museum (CU)

TABLE 2.—Means (± standard deviation) for adult males for each of the OTUs utilized in this study that includes four or more specimens.

OTU#	N	Total Length	Tail	Hind foot	Condylobasal Length	Zygomatic Breadth	Mastoid Breadth	Nasal Breadth	Frontal Square Length	Frontal Square Breadth	Orbital Length	Maxillary Visibility
4	8	269.1±13.8	81.9±09.6	34.2±1.2	48.21±1.22	30.11±1.47	28.15±0.93	9.91±0.49	4.91±0.74	1.61±0.42	16.12±0.52	0.9±0.4
6	7	261.0±16.8	77.1±04.5	32.1±1.6	48.03±1.89	30.97±0.97	27.57±0.96	9.99±0.22	4.44±0.48	1.61±0.26	16.03±0.72	0.9±0.4
7	5	257.2±11.9	76.4±05.2	32.4±0.9	46.72±1.42	30.00±1.46	27.38±1.15	9.86±0.25	3.72±0.59	1.64±0.42	15.68±0.60	1.0±0.0
10	5	266.8±10.2	83.8±03.9	33.0±1.0	47.80±0.89	29.84±1.49	27.36±0.50	9.78±0.41	4.98±0.76	1.52±0.29	16.14±0.21	1.0±0.0
14	4	272.7±12.4	82.7±08.0	32.7±2.2	46.62±0.81	29.52±1.15	26.00±0.35	9.97±0.29	3.65±0.50	1.90±0.29	15.70±0.50	0.3±0.5
16	4	264.0±12.1	76.0±08.8	32.5±3.7	46.37±1.60	29.85±0.97	26.17±0.42	10.20±0.16	2.90±0.27	2.15±0.13	15.27±0.25	0.0±0.0
17	8	265.7±09.9	85.0±03.9	34.1±0.6	48.11±1.86	31.12±2.02	27.74±1.40	11.15±0.61	3.59±0.29	1.80±0.26	15.69±0.59	0.0±0.0
19	4	265.0±15.8	75.5±06.5	32.2±1.0	47.45±2.24	29.67±2.12	26.90±1.92	10.27±0.62	3.62±0.47	1.95±0.26	16.22±1.01	0.2±0.5
21	4	270.2±22.9	78.2±11.6	34.0±2.6	47.32±1.36	31.00±1.57	26.90±1.02	10.85±0.54	3.82±0.68	2.20±0.26	15.12±0.26	0.0±0.0
23	6	263.7±08.6	72.2±06.8	33.2±1.8	48.37±0.80	31.75±0.61	26.92±0.84	10.20±0.55	3.87±0.60	1.78±0.22	15.55±0.71	0.5±0.5
25	10	270.1±12.6	75.6±06.0	34.3±1.3	47.21±2.19	30.12±1.52	27.25±1.44	10.49±0.53	4.07±0.48	1.95±0.43	15.76±0.49	0.9±0.3
26	5	261.4±06.5	79.4±07.1	33.0±1.2	47.00±0.68	30.30±0.68	26.78±0.79	10.14±0.34	3.40±1.00	1.80±0.48	15.54±0.26	0.6±0.5
28	5	260.4±09.6	77.8±02.6	34.2±1.3	46.40±2.06	29.47±1.19	26.42±1.44	10.00±0.32	3.32±0.34	1.70±0.35	15.85±0.67	0.5±0.5
30	13	267.5±11.1	70.4±06.2	33.8±2.3	46.35±1.73	30.30±1.49	27.02±1.40	10.50±0.45	4.07±0.57	1.91±0.55	15.56±0.76	0.5±0.5
31	4	278.2±09.0	80.0±04.8	33.2±1.0	48.95±1.01	31.10±1.16	27.92±0.56	10.67±0.57	4.22±0.50	1.72±0.71	16.32±0.55	0.5±0.5
33	16	262.8±19.5	75.6±07.2	32.7±3.3	47.70±2.90	30.97±2.36	27.28±1.56	10.58±0.59	4.47±0.94	1.81±0.54	16.29±0.96	0.4±0.5
35	6	268.3±06.4	75.2±10.2	32.8±1.7	47.17±1.52	30.97±1.04	27.05±0.44	10.40±0.59	4.38±0.52	2.00±0.17	15.68±0.69	0.3±0.5
38	5	256.0±08.1	68.0±07.2	31.2±1.3	46.62±0.36	30.24±1.24	26.82±1.04	10.20±0.59	3.84±0.51	1.94±0.38	15.44±0.42	0.3±0.4
40	8	279.4±0.48	81.0±06.1	33.2±1.8	49.04±1.02	32.51±1.36	28.06±1.32	11.16±0.76	4.54±0.37	2.09±0.50	16.36±0.72	0.2±0.4
43	6	324.3±24.8	93.7±11.1	35.3±3.6	54.47±0.98	34.88±0.98	30.80±1.28	10.67±0.45	4.07±0.69	2.05±0.47	18.50±0.74	0.7±0.5
46	4	293.7±10.5	82.7±05.6	36.5±1.7	54.07±2.08	35.20±0.77	30.92±0.94	10.95±1.01	4.50±0.88	2.07±0.35	18.37±0.57	0.2±0.5
48	7	301.0±15.0	79.0±10.3	36.3±1.1	55.74±2.22	35.53±1.70	32.16±1.79	10.94±0.68	4.41±1.10	1.76±0.55	18.20±1.02	0.9±0.4
49	4	284.2±22.2	81.0±04.2	33.7±1.3	53.96±4.37	33.67±3.17	29.05±2.26	10.52±0.66	4.50±0.47	1.60±0.40	17.13±1.64	0.8±0.4
50	11	320.3±17.0	84.8±11.4	38.3±2.9	57.16±3.77	35.18±2.85	31.58±1.89	11.06±0.62	4.40±0.70	2.09±0.41	17.80±1.30	1.0±0.0
51[1]	5	312.8±17.5	91.2±07.9	36.8±1.3	54.24±0.45	35.42±0.96	31.48±0.66	10.98±0.26	4.64±0.32	2.20±0.55	18.06±1.16	0.6±0.5
55	4	320.5±08.4	94.8±03.5	40.3±2.2	59.13±2.19	36.12±0.70	33.28±0.59	11.23±0.22	4.78±0.66	2.50±0.14	19.23±0.89	1.0±0.0
59	9	288.7±16.3	75.1±06.0	35.1±2.3	54.74±2.00	34.04±1.75	29.31±1.25	10.51±0.48	4.97±0.26	2.18±0.35	17.87±0.85	1.0±0.0
61	11	308.5±09.0	84.1±04.7	38.2±1.3	57.25±0.82	36.02±0.92	31.81±0.84	10.95±0.24	5.27±0.71	2.39±0.29	17.94±0.52	1.0±0.0
65	6	282.0±23.1	84.0±07.8	34.8±2.7	53.62±2.26	33.40±2.01	28.83±1.79	10.32±0.38	4.43±0.96	1.88±0.42	17.47±1.25	1.0±0.0
66	8	294.8±21.4	86.3±11.2	35.1±1.8	53.00±1.58	32.73±1.36	27.91±0.84	10.30±0.30	3.63±0.38	2.80±0.48	17.24±0.30	0.4±0.5
67	4	301.5±09.1	91.8±04.4	34.5±1.3	56.73±1.84	35.83±1.15	31.18±0.56	10.76±0.10	6.20±0.83	1.93±0.43	18.90±0.86	1.0±0.0
69	4	305.0±22.0	93.8±08.8	35.0±1.2	55.55±1.98	34.95±1.87	30.55±2.13	10.90±0.58	6.05±0.78	2.00±0.50	18.13±1.14	0.5±0.6
70	8	319.3±29.1	92.6±11.9	35.3±1.3	56.50±1.62	36.09±0.80	30.84±0.65	11.31±0.34	6.31±0.57	2.33±0.21	18.14±0.43	0.9±0.4
71	6	268.0±13.3	83.5±07.4	33.3±2.0	47.77±1.67	31.00±0.91	28.43±0.83	10.02±0.36	5.20±1.08	1.65±0.30	16.43±0.41	0.8±0.4
72	5	274.0±14.8	82.2±13.4	34.6±0.9	48.02±1.98	31.12±1.37	28.72±1.27	10.22±0.32	4.18±1.08	1.36±0.52	16.34±0.38	1.0±0.0
73	6	268.3±09.8	78.7±06.4	31.7±1.6	48.45±1.74	30.92±2.02	28.08±1.74	10.00±0.37	4.28±0.74	1.62±0.33	16.23±0.24	0.8±0.4
75	4	263.3±17.4	75.8±07.0	30.5±2.5	47.58±2.50	30.45±1.60	27.38±1.35	9.98±0.47	4.60±0.35	1.38±0.22	15.53±1.04	0.8±0.5
78	6	251.3±08.8	72.2±04.3	29.8±1.3	45.55±1.96	29.18±0.66	25.62±1.11	9.68±0.59	3.53±1.27	1.87±0.46	14.85±0.52	0.8±0.4
81	5	311.6±23.6	90.0±08.7	36.0±3.2	54.28±3.54	34.66±2.94	30.50±1.55	10.54±0.53	4.80±1.31	1.92±0.25	17.36±0.83	1.0±0.0

[1] From eastern edge of hybrid zone (Heaney, 1979).

Field Museum of Natural History (FMNH)
Kearney State College (KSC)
Museum of Natural History, University of Kansas (KU; Vertebrate Paleontology, KUVP)
Museum of the High Plains, Fort Hays State University (MHP)
Bell Museum of Natural History, University of Minnesota (MMNH)
Museum of Natural History, Michigan State University (MSU)
Museum of Vertebrate Zoology, University of California (MVZ)
University of Nebraska State Museum (NSM)
Oklahoma State University (OSU)
Stovall Museum, University of Oklahoma (SM)
Museum of Natural History, University of Illinois (UIMNH)
University of Missouri at Columbia (UMC)
Museum of Zoology, University of Michigan (UMMZ)
United States National Museum of Natural History (USNM)

SYSTEMATIC ACCOUNTS OF SPECIES AND SUBSPECIES

Geomys bursarius (Shaw, 1800)

Plains Pocket Gopher

Geomys bursarius bursarius (Shaw, 1800)

1800. *Mus bursarius* Shaw, Trans. Linn. Soc. London 5:227. Type locality Elk River, Sherburne County, Minnesota (originally cited as "the interior of Canada"; fixed by Swenk, 1939).
1817. *Diplostoma fusca* Rafinesque, Amer. Monthly Mag. 2:44. Type from Missouri River region.
1817. *Diplostoma alba* Rafinesque, Amer. Monthly Mag. 2:44. Type from Missouri River region.
1821. *Mus saccatus* Mitchill, Med. Repos. (n.s.) [New York], 6(21):249. Type from "area bordering on Lake Superior."
1825. *Ascomys canadensis* Lichtenstein, Abh. K. Akad. Wiss., Berlin, for 1822, p. 20. Type from "Canada."
1829. *Geomys bursarius* Richardson, Fauna Boreali-Americana 1:203. First use of name combination.
1939. *Geomys bursarius majusculus* Swenk, Missouri Valley Fauna 1:6. Type from Lincoln, Lancaster County, Nebraska.
1958. *Geomys bursarius missouriensis* McLaughlin, Los Angeles County Mus. Cont. Sci. 19:1. Type from 2 mi. N Manchester, St. Louis County, Missouri.

Type specimen.—Uncertain; perhaps the specimen from the Bullock collection, now in the Rijksmuseum van Natuurlijke Historie, Leiden (see Merriam, 1895:123-127).

Distribution.—Occurs principally in tall-grass prairie in the northeastern portion of the Great Plains west of the Mississippi River (Fig. 1).

Description.—For a complete description of *Geomys,* see Merriam (1895). This description and those following refer to adult females. Size large for genus; adult females averaging head and body length and condylobasal length from 170 mm and 44.4 mm (in northwestern Wisconsin) to 210 mm and 50.5 mm (in northeastern Iowa), respectively (Fig. 3). Skull large, robust (Fig. 2A); zygomata broad, widely divergent anteriorly; sagittal crest narrow and usually high; rostrum long (both relatively and absolutely); frontal-premaxillary suture on dorsum falling anterior to or reaching (not exceeding) a line drawn between the anterior-most points in the orbits; mastoid processes long, projecting at an angle approximately 20° from horizontal; braincase oval; naso-frontal region usually domed slightly; anterior root of zygomatic arches sloping back strongly. Face of upper incisors strongly bisulcate; minor sulcus fine and close to inner edge of tooth; principal sulcus much deeper and wider, and lying on or slightly external to median line; enamel face rounded externally and between sulci. Incisors procumbent. Upper premolar bilobate, curved, sloping forward basally, and concave anteriorly; last molar curving backwards basally, and concave

posteriorly. M^1 and M^2 curved backward, M^1 slightly and M^2 more strongly. P_4 bilobate, large, curving forward basally, concave anteriorly; M_1 through M_3 decreasing progressively in length, and increasing in basal curvature towards posterior; M_3 concave posteriorly.

Color a rich chocolate or chestnut brown dorsally, hairs without dark tips; slightly to considerably lighter ventrally; ventrum often with silver cast. Dorsum sometimes with a medial darkened region from snout to base of tail, 10 to 15 mm wide; this dorsal "stripe" is most conspicuous in populations in Kansas and Missouri, and only barely discerna-

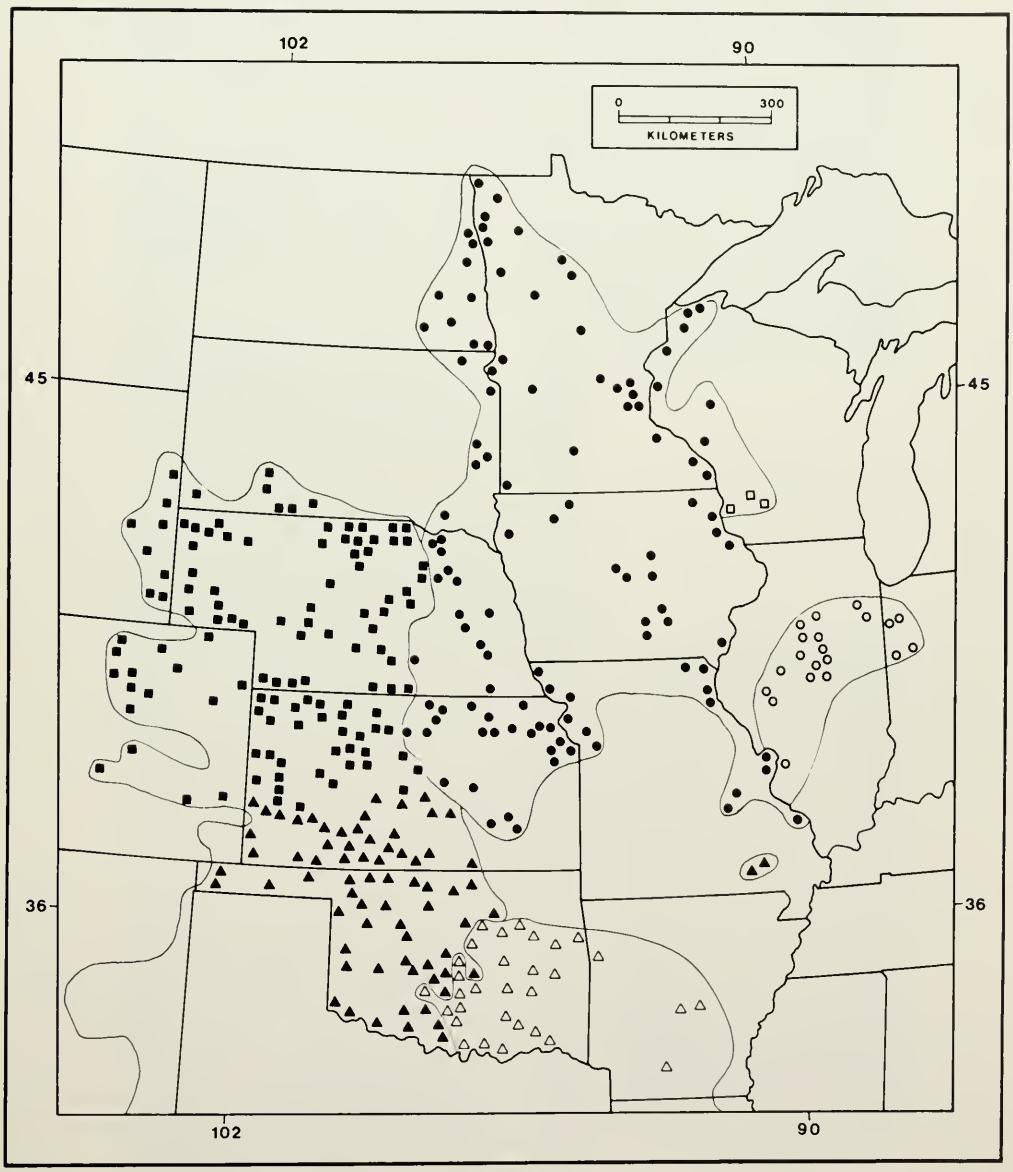

FIG. 1.—Map showing distribution of *Geomys* in the central and northern Great Plains. Solid circles = *G. bursarius bursarius;* open circles = *G. b. illinoensis;* open squares = *G. b. wisconsinensis;* solid squares = *G. lutescens lutescens;* solid triangles = *G. l. major;* open triangles = *G. breviceps sagittalis.*

ble in Nebraska, Iowa, and most of Minnesota. Pelage near mouth often white. Dorsal surface of fore- and hindfeet with white fur (hindfeet sparsely covered); white fur often on ventral base of forelimbs, sometimes extending to base of humerus. Mystacial vibrissae stiff, relatively fine, 5-30 mm in length; supraorbital and preauricular vibrissae very fine, few in number, up to 10 mm in length. Color of vibrissae ranges from light to dark brown. Tail moderately long (36-42% of head and body) and thick, with blunt tip. Basal quarter of tail usually well furred, with density of hair decreasing toward tip. Distal portion (half to four-fifths) often with white hairs, sometimes nearly naked. Melanism rare, at frequencies less than 1% in known populations.

Forefoot large with five stout claws; digits III, IV, II, V, and I with progressively shorter claws. Hindfoot not unusually large, claws normal.

Diagnosis and comparisons.—Differs from *G. breviceps* in having much greater overall size; dorsal color without "peppering" due to dark distal bands on hairs; sagittal crest prominent and high, rather than a poorly-defined ridge 4-5 mm wide between the temporal crests; zygomatic arches wider at anterior than posterior angles, rather than approximately equal in width; auditory bullae proportionately longer, less dome-shaped. Differs from *G. lutescens* in having rich brown cast to dorsal pelage, rather than having yellowish cast; temporal ridges fused into a sagittal crest in adult females, rather than being separated by a ridge 2-3 mm wide defined by the temporal ridges; rostrum absolutely and relatively longer; frontal-premaxillary suture on dorsum usually falling anterior to or reaching (not exceeding) a line drawn between anteriormost points in the orbits; mastoid processes longer, less closely appressed to skull; braincase oval, not rectangular; nasofrontal junction domed, not flat. Differs from *G. bursarius illinoensis* in being smaller, having a proportionately shorter rostrum and shorter tail (mean 39.1%; 33.9 to 44.3% length of head and body), and having brown rather than slate-gray ("melanistic") fur in most individuals. Differs from *G. bursarius wisconsinensis* in having a proportionately shorter tail and in having the anterior portion of the frontals forming a rectangle rather than a square (Jackson, 1961). Baculum long (mean = 11.3 mm) with proportions typical for the species-group (Fig. 15; Table 8).

Specimens examined.—Iowa: *Clay Co.:* no specific locality (2 UMMZ); *Clayton Co.:* 4 mi. NE Garbin (1 SM); 4 mi. E Monona (2 SM); Monona (7 SM); *Dubuque Co.:* 4 mi. NE Bankston (1 SM); *Emmett Co.:* 3½ mi. S, 2¾ mi. E Wallingford (1 KU); *Grundy Co.:* 4½ mi. S, 2½ mi. W Wellsburg (1 KU); *Mahaska Co.:* 2½ mi. E New Sharon (1 KU); 2 mi. N, 3 mi. E Oskaloosa (1 KU); *Marion Co.:* Knoxville (11 USNM); *Marshall Co.:* 3 mi. W Green Mountain (1 KU); SE ¼ sec. 2, T82N, R17W (1 KU); *Monroe Co.:* 1½ mi. N Melrose (1 KU); *Plymouth Co.:* 3 mi. N Le Mars; *Story Co.:* 1 mi. N Ames (1 MSU); SW ¼ sec. 10, T83N, R24W (1 KU); *Winneshiek Co.:* Decorah (1 UMMZ).

Kansas: *Atchison Co.:* 3 mi. N Cummings (2 KU); 1½ mi. S Muscotah (1 KU); *Butler Co.:* 8 mi. W Rosalia (2 KU); *Cloud Co.:* 2¾ mi. N, 2 mi. E Jamestown (6 KU); 4 mi. E Jamestown (1 KU); *Douglas Co.:* 1¾ mi. N, 1½ mi. E Lawrence (4 MHP); ¼ mi. N, 1½ mi. E Lawrence (1 KU); Lawrence (8 KU); ⅛ mi. W Lawrence (1 KU); 2½ mi. W Lawrence (1 KU); 1 mi. S, 4 mi. W Lawrence (2 KU); no specific locality (2 KU); *Greenwood Co.:* ¼ mi. E Hamilton (1 KU); ⅒ mi. E Hamilton (1 KU); Hamilton (6 KU); ¼ mi. S Hamilton (1 KU); ½ mi. S Hamilton (2 KU); 1 mi. S Hamilton (1 KU); 8½ mi. S Toronto (2 KU); no specific locality (2 KU); *Jackson Co.:* Birmingham (1 KU); *Jefferson Co.:* 1 mi. NW Midland (1 KU); *Jewell Co.:* NE ¼ sec. 12, T1S, R6W (2 MHP); *Leavenworth Co.:* Fort

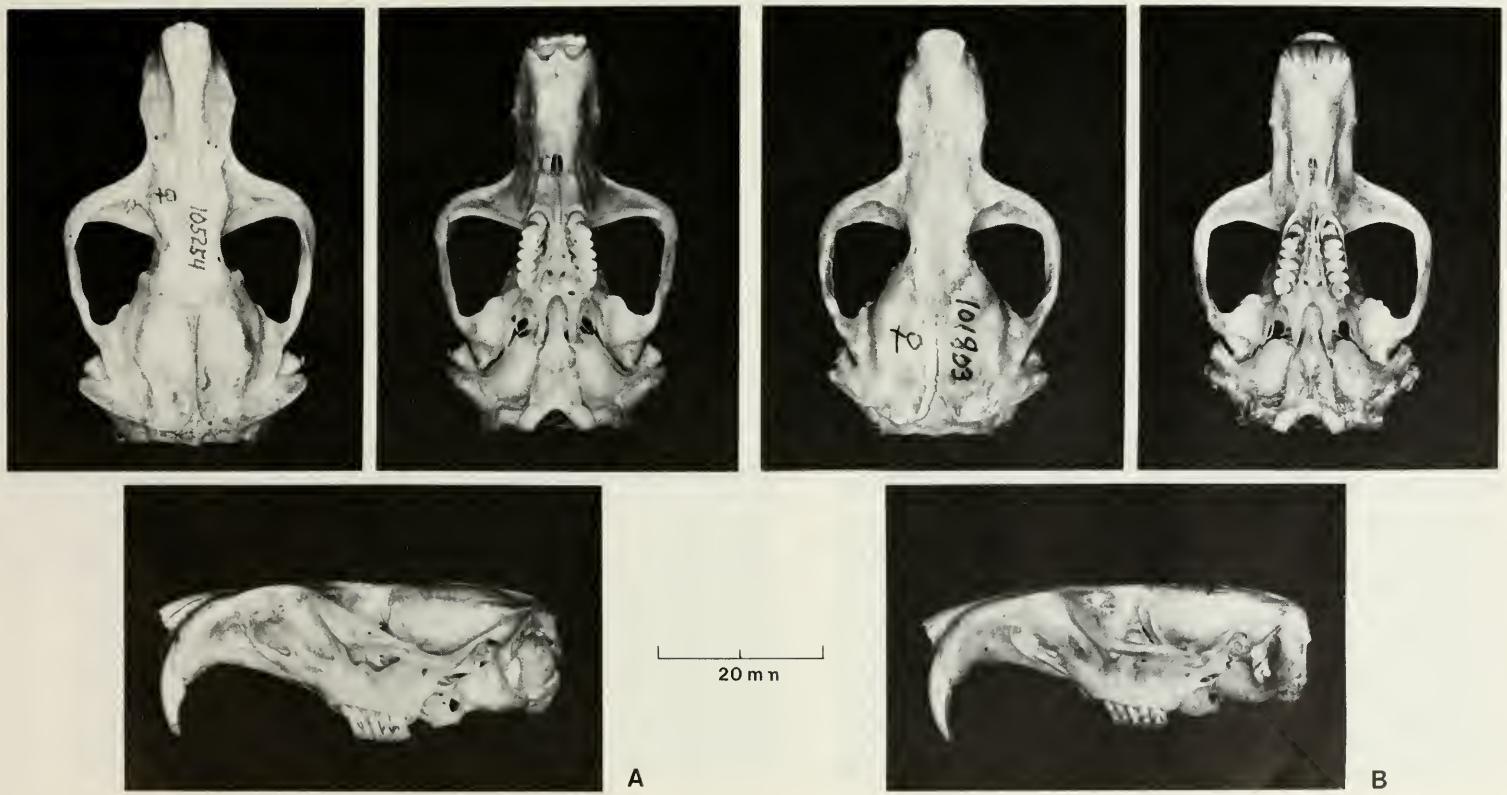

FIG. 2.—Photographs of crania of adult females of: A. *Geomys bursarius bursarius;* B. *G. bursarius illinoensis.*

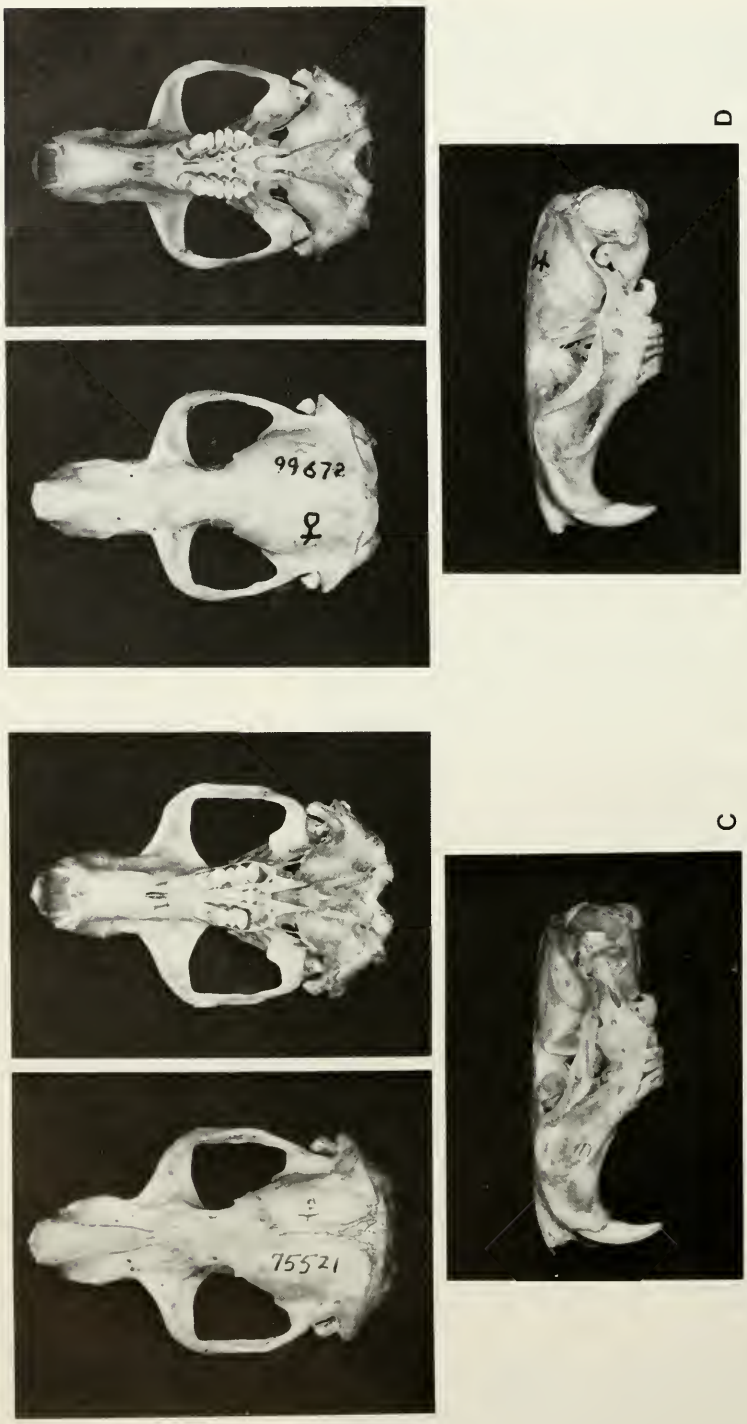

FIG. 2.—*(continued).* Photographs of crania of adult females of: C. *Geomys lutescens lutescens;* D. *G. lutescens major.*

Leavenworth (1 KU); no specific locality (1 KU); *Marion Co.:* 1½ mi. NE Lincolnville (1 KU); *Marshall Co.:* ½ mi. N, 1 mi. W Blue Rapids (2 KU); Waterville (2 KU); *McPherson Co.:* 1 mi. S, ½ mi. W Lindsborg (1 KU); *Mitchell Co.:* 1 mi. N, 2 mi. E Beloit (1 KU); ½ mi. S, 3½ mi. W Beloit (8 KU); *Nemaha Co.:* 2 mi. N Sabetha (1 MSU); *Osborne Co.:* ½ mi. S, 8 mi. E Osborne (2 KU); *Pottawatomie Co.:* 1 mi. E Olsburg (1 KU); 1½ mi. N, 1 mi. W Olsburg (1 KU); Onaga (3 USNM); *Republic Co.:* Scandia (4 KU); 2 mi. N, ½ mi. W Scandia (1 KU); *Riley Co.:* 5½ mi. N, 2½ mi. E Randolph (2 KU); 5½ mi. N, 1½ mi. E Randolph (5 KU); ½ mi. S, ¼ mi. W Randolph (1 KU); *Washington Co.:* 7¾ mi. N, 3½ mi. W Washington (1 KU); *Wyandotte Co.:* Wyandotte (1 MHP).

Minnesota: *Anoka Co.:* 5½ mi. N, 1 mi. W Lino Lakes (1 KU); Carlos Avery Game Mgmt. Area (1 KU); *Becker Co.:* SW ¼ sec. 24, T139N, R42W (1 MMNH); *Beltrami Co.:* 11 mi. N Bemidji (1 BSU); SE¼ sec. 5, T148N, R35W (2 MMNH); *Brown Co.:* SW ¼ sec. 7, T110N, R21W (1 MMNH); *Cass Co.:* Cass Lake (1 USNM); *Goodhue Co.:* Goodhue (1 MMNH; 1 UMMZ); *Hennepin Co.:* Minneapolis (1 MMNH); *Houston Co.:* La Crescent (1 USNM); *Kittson Co.:* Karlstad (1 MMNH); St. Vincent (1 USNM); *Marshall Co.:* 1 mi. N Alvarado (1 MMNH); *Morrison Co.:* 1 mi. S Pillager (1 MMNH); *Norman Co.:* NW ¼ sec. 13, T145N, R44W (1 MMNH); *Pennington Co.:* no specific locality (1 BSU); *Polk Co.:* 4½ mi. S Fisher (1 MMNH); NW ¼ sec. 6, T149N, R39W (1 MMNH); 1½ mi. S Alvarado (1 MMNH); *Ramsey Co.:* St. Paul (3 KU; 22 MMNH); *Rock Co.:* 5 mi. WSW Luverne (1 MSU); *Sherburne Co.:* Elk River (5 KU, 6 USNM); 6 mi. SE St. Cloud (1 UMMZ); *Swift Co.:* NE ¼ sec. 2, T120N, R40W (2 MMNH); *Traverse*

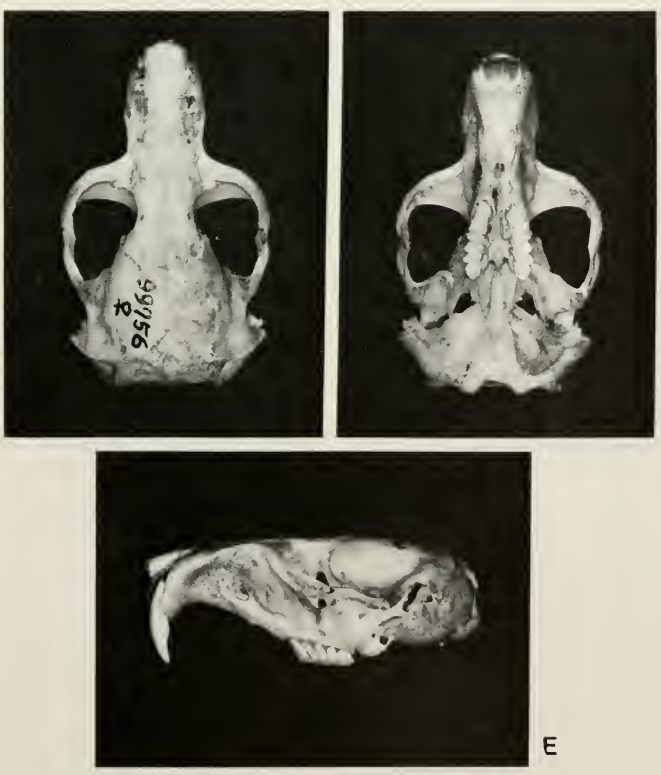

Fig. 2.—*(continued).* Photographs of crania of adult female of: E. *Geomys breviceps sagittalis.*

Co.: near Brown's Valley (1 USNM); Wheaton (1 MMNH); *Winona Co.:* 8 mi. S, 5 mi. W Winona (1 MMNH).

Missouri: *Andrew Co.:* 1 mi. E Flag Springs (1 UMC); *Atchison Co.:* 5 mi. S, 2½ mi. W Rock Port (1 UMC); *Buchanan Co.:* St. Joseph (1 UMC); 5 mi. SW St. Joseph (3 UMC); *Clark Co.:* Kahoka (2 UMC); no specific locality (4 UMC); *Clay Co.:* Smithville (1 UMC); *Crawford Co.:* Steelville (1 UMC); *Franklin Co.:* 2½ mi. E Sullivan (1 SM); Sullivan (1 UMC); *Holt Co.:* Mound City (1 UMC); no specific locality (1 UMC); *Jackson Co.:* Buckner (1 UMC); no specific locality (1 UMC); *Lewis Co.:* Wakonda State Park (1 KU); no specific locality (2 UMC); *Marion Co.:* no specific locality (2 UMC); *Perry Co.:* Perryville (1 UMC); *Scotland Co.:* no specific locality (1 UMC); *St. Charles Co.:* 3½ mi. S Orchard Farm (1 KU); no specific locality (3 UMC); *St. Louis Co.:* Afton (2 UMC); Baden (1 UMC); ¼ mi. N Black Jack (1 UMC); 2 mi. E Creve Coeur Lake (1 UMC); 1½ mi. S Creve Coeur Lake (1 UMC); 2½ mi. NE Cross Keys (2 KU); 1¼ mi. NW Cross Keys (1 KU); Florissant (4 KU); Ladue (1 UMC); 1 mi. W Lindberg (1 UMC); St. Louis (2 USNM); Clayton Rd. and Hwy. 340 (1 UMC); no specific locality (4 UMC).

Nebraska: *Adams Co.:* Hastings (4 AMNH); *Antelope Co.:* ¼ mi. N, 2¾ mi. E Oakdale (5 UMMZ); 2¾ mi. E Oakdale (5 FMNH); W edge Oakdale (8 SM); ½ mi. W Oakdale (3 SM); ⅜ mi. S, ⅝ mi. W Oakdale (5 KU); ⅜ mi. S, ⅞ mi. W Oakdale (6 KU); ½ mi. S, 1½ mi. E Oakdale (1 UMMZ); 2⅛ mi. S Oakdale (1 SM); 1 mi. W Tilden (2 SM); 5 mi. W Tilden (1 KU); *Butler Co.:* 4 mi. E Rising City (1 KU); *Dodge Co.:* Ames (1 USNM); *Gage Co.:* 2 mi. S, ½ mi. E Barnston (1 KU); *Knox Co.:* ½ mi. N, 3 mi. W Center (1 KU); ½ mi. S, 1 mi. W Niobrara (3 KU); 2½ mi. S, 9 mi. W Niobrara (2 KU); mouth of Niobrara River (1 USNM); Verdigre (1 USNM); *Lancaster Co.:* ½ mi. S College View (1 KU); 5 mi. N Lincoln (1 KU); 5¾ mi. E Lincoln (1 KU); Lincoln (2 KU, 10 NSM); 2 mi. S, 1 mi. E Malcolm (1 NSM); 3 mi. S Malcolm (4 NSM); *Madison Co.:* Norfolk (2 USNM); *Pierce Co.:* 7⅝ mi. N Meadow Grove (1 KU); *Platte Co.:* Columbus (1 USNM).

North Dakota: *Barnes Co.:* Valley City (1 USNM); *Cass Co.:* Casselton (1 USNM); *Grand Forks Co.:* Grand Forks (1 USNM); Manvel (1 USNM); *La Moure Co.:* La Moure (1 USNM); *Ransom Co.:* Lisbon (1 USNM); *Richland Co.:* Blackmir (1 USNM); 5 mi. E Fairmount (2 USNM); Lidgerwood (6 USNM); *Trail Co.:* Portland (7 USNM).

South Dakota: *Bon Homme Co.:* 4½ mi. E Scotland (1 SM); *Brookings Co.:* 5½ mi. N, 1 mi. E Volga (1 MMNH); 5 mi. N, 3 mi. W Volga (2 MMNH); 4 mi. N, 2 mi. W Volga (2 MMNH); 2½ mi. S, 3 mi. W Volga (1 MMNH); 3½ mi. S, 2½ mi. W Volga (1 MMNH); 3½ mi. S, 3 mi. W Volga (1 MMNH); 3½ mi. S, 4½ mi. W Volga (1 MMNH); 4½ mi. S, 1¼ mi. W Volga (1 MMNH); 5 mi. S, 1 mi. W Volga (2 MMNH); 6½ mi. S, 1½ mi. E Volga (1 MMNH); 7½ mi. S, 2¾ mi. E Volga (2 MMNH); 7½ mi. S, 2½ mi. E Volga (1 MMNH); 7½ mi. S, 2 mi. E Volga (1 MMNH); *Grant Co.:* 6 mi. N Milbank (4 KU); *Lake Co.:* 1 mi. S, 1 mi. E Madison (1 MMNH); 1½ mi. S, 1 mi. E Madison (1 MMNH); *Marshall Co.:* Roy Lake State Park (3 KU); *Moody Co.:* 14 mi. S, 1⅔ mi. E Brooking (1 MMNH); 12 mi. S, ½ mi. E Brooking (1 MMNH); 3½ mi. S, 1½ mi. W Volga (1 MMNH).

Wisconsin: *Bayfield Co.:* 4 mi. E Iron River (1 UIMNH); 5 mi. W Iron River (1 UIMNH); 7 mi. W Iron River (1 UIMNH); *Burnett Co.:* Danbury (1 USNM); *Chippewa Co.:* Anson Township (3 USNM); *Douglas Co.:* 3 mi. S, 3 mi. W Brule (8 UIMNH); 3 mi. N, 3 mi. E Solon Springs (1 UIMNH); Solon Springs (1 USNM); *Polk Co.:* ½ mi. N Dresser (1 UIMNH); ½ mi. S, 1 mi. W Dresser (2 UIMNH); 3 mi. S St. Croix

Falls (1 UIMNH); *Trempealeau Co.:* 4 mi. N Arcadia (2 UIMNH).

Geomys bursarius illinoensis Komarek and Spencer, 1931

1931. *Geomys bursarius illinoensis* Komarek and Spencer, J. Mammal. 12:405.
1936. *Geomys illinoensis* Lyon, Amer. Midl. Nat. 17:216. First use of name combination.
1941. *Geomys bursarius illinoensis* Necker and Hatfield, Bull. Chicago Acad. Sci. 6:51.

Type specimen.—Chicago Academy of Sciences 713, from 1 mi. S Momence, Kankakee County, Illinois. Type now housed in the Field Museum of Natural History.

Distribution.—Occurs in tall-grass prairie—oak-hickory savannah community (Küchler, 1964) in eastern and central Illinois and west-central Indiana (Fig. 1).

Diagnosis and comparisons.—May be distinguished from *G. breviceps, G. bursarius bursarius,* and *G. lutescens,* as noted in the *G. b. bursarius* description and diagnosis. Differs from *G. bursarius wisconsinensis* in being larger with a proportionately longer rostrum (Fig. 2B) and tail (40 to 44% length of head and body), and having slate-gray ("melanistic") pelage in nearly all individuals.

Specimens examined.—Illinois: *Cass Co.:* 2⅘ mi. ESE Bluff Springs (1 KU); *DeWitt Co.:* 1½ mi. ENE Clinton (1 UIMNH); 2 mi. E Clinton (1 KU); 1½ mi. E Clinton (1 UIMNH); 1 mi. E Clinton (1 UIMNH); Clinton (1 UIMNH, 5 USNM); 1 mi. S, 1 mi. E Clinton (2 UIMNH); 1 mi. SSE Clinton (1 UIMNH); ⅔ mi. NE Junction US Rt. 51 and 54 (1 KU); *Kankakee Co.:* 1½ mi. S, 1½ mi. W Kankakee (1 UIMNH); *LaSalle Co.:* ⅘ mi. S Lostant (1 UIMNH); *Logan Co.:* 5 mi. E Lincoln (1 UIMNH); 2 mi. E Lincoln (1 UIMNH); *Madison Co.:* Collinsville (3 KU); *Marshall Co.:* 2 mi. E Lacon; *Mason Co.:* 4½ mi. S Bath (1 KU); 3 mi. E Havanna (1 KU); Havanna (1 USNM); *McLean Co.:* 10 mi. N Bloomington (1 UIMNH); 2 mi. SE Bloomington (1 KU); 2 mi. W Hudson (2 UIMNH); 4 mi. E McLean (2 UIMNH); 1 mi. S McLean (1 UIMNH); 9 mi. N Normal (1 UIMNH); 5½ mi. N Normal (1 UIMNH); 3 mi. N Normal (1 UIMNH); Normal (5 KU); *Morgan Co.:* 5 mi. NE Jacksonville (1 UIMNH); *Tazewell Co.:* Lilly (1 UIMNH); *Will Co.:* 2 mi. W Wilmington (1 UMMZ); *Woodford Co.:* 1 mi. W Benson (1 UIMNH); 4 mi. N El Paso (1 UIMNH); 2½ mi. N El Paso (1 UIMNH); 2 mi. N El Paso (1 UIMNH); 6 mi. N Eureka (1 UIMNH); 1 mi. NW Kappa (1 UIMNH); 1 mi. S, 8 mi. W Minonk (1 UIMNH).

Indiana: *Jasper Co.:* 3 mi. E Roselawn (1 USNM); 2 mi. E Roselawn (1 UIMNH); *Newton Co.:* Lake Village (1 UMMZ); 1 mi. E Roselawn (1 UIMNH, 1 USNM); Junction US Rt. 10 and 55 (1 USNM); no specific locality (1 UMMZ); *Tippecanoe Co.:* Battle Ground (1 UMMZ, 6 USNM); Lafayette (2 USNM); *Warren Co.:* 1½ mi. NE Pine Village (1 USNM).

Geomys bursarius wisconsinensis Jackson, 1957

1957. *Geomys bursarius wisconsinensis* Jackson, Proc. Biol. Soc. Washington 70:33.

Type specimen.—USNM 243055, taken on 13 September 1922 at Lone Rock, Richland County, Wisconsin.

Distribution.—Occurs in southwestern Wisconsin, in the vicinity of the north bank of the Wisconsin River, in oak savannah intermixed with maple-basswood forest (Fig. 1).

Diagnosis and comparisons.—Differs from other *G. bursarius* in having that portion of the frontals which projects between the premaxillaries contact the nasals in the shape of a square rather than an elongated rectangle; tail moderately long (43.2% length of head and body). Comparisons with other taxa as noted above.

Specimens examined. — Wisconsin: *Crawford Co.:* 1 mi. W Wauzeka (5 UIMNH); *Richland Co.:* ½ mi. E Gotham (3 SM); Gotham (3 SM); Lone Rock (7 MMNH, 2 USNM).

Geomys breviceps Baird, 1855
Southern Plains Pocket Gopher

Geomys breviceps breviceps Baird, 1855

1855. *Geomys breviceps* Baird, Proc. Acad. Nat. Sci. Philadelphia 7:335.

Type specimen.—USNM 156 (skin)/1138 (skull), obtained in 1852 at Prairie Mer Rouge, Morehouse Parish, Louisiana.

Distribution.—Extralimital to study area; vicinity of Mer Rouge, Louisiana only (see Lowery, 1974).

Diagnosis and comparisons.—See diagnosis of *G. b. sagittalis.*

Specimens examined. — Louisiana: *Morehouse Parish:* Prairie Mer Rouge (1 USNM, holotype); plus approximately 45 others in USNM from the vicinity of the type locality.

Geomys breviceps sagittalis Merriam, 1895

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1938. *Geomys breviceps brazensis* Davis, J. Mammal. 19:489. Type from 5 mi. E Kurten, Grimes County, Texas.
1940. *Geomys breviceps dutcheri* Davis, Texas Agr. Exp. Sta. Bull. 590:12. Type from Fort Gibson, Muskogee County, Oklahoma.
1940. *Geomys breviceps terricolus* Davis, Texas Agr. Exp. Sta. Bull. 590:17. Type from 1 mi. N Texas City, Galveston County, Texas.
1940. *Geomys breviceps pratincolus* Davis, Texas Agr. Exp. Sta. Bull. 590:18. Type from 2 mi. E Liberty, Liberty County, Texas.
1940. *Geomys breviceps ludemani* Davis, Texas Agr. Exp. Sta. Bull. 590:19. Type from 7 mi. SW Fannett, Jefferson County, Texas.

Type specimen.—USNM 32936 (skin)/44957 (skull), obtained 28 March 1892 at Clear Creek, Galveston Bay, Galveston County, Texas.

Distribution.—Ranges from southern Texas near Galveston Bay (extralimital; see Honeycutt and Schmidly, 1979) to northeastern Oklahoma and eastern Arkansas (Fig. 1).

Description.—Size small for genus; adult females (within study area) averaging head and body length from 145 mm to 155 mm, condylobasal length 39.3 mm to 40.2 mm (Fig. 3). Skull (Fig. 2E) small, sturdy; zygomatic arches only slightly broader anteriorly than at posterior angle, or equal in width; interorbital region flat or concave; rostrum absolutely and relatively short, moderately narrow; temporal crests separated medially by poorly defined ridge 4-5 mm wide; mastoid processes short, nearly as broad (at base) as long; foramen rotundum relatively low on alisphenoid, not obscured in lateral view by zygomatic arch; braincase smoothly rounded. Incisors as in *G. bursarius*, but less procumbent. P^4 and P_4 usually straight in lateral profile, less often slightly concave. Molars as in *G. bursarius.* Forefeet as in *G. bursarius*, although proportionately less enlarged. Tail shape and pelage density as in *G. bursarius;* tail length moderate, 41-49% of head and body length.

Color of dorsal pelage variable, showing a general cline from medium brown with only a trace of yellow in gophers from the eastern quarter of Oklahoma, to a lighter brown suffused with a yellow (in the north) or orange (in the south) tone suffused through both dorsal and ventral pelage along the western margin of the distribution of the species (from Payne through Love and Marshall counties). "Peppering" due to black tips on dorsal hairs prominent in all populations. Mid-dorsal region sometimes showing darkening; development of this is variable within populations, but seems never to be so prominent as in some populations of *G. bursarius* and *G. lutescens.* Ventral pelage often with a silver sheen, and often with white spotting.

Diagnosis and comparisons.—Differs from *G. bursarius* as noted above. Differs from *G. lutescens* in being generally smaller; temporal crests separated by poorly defined ridge 4-5 mm wide rather than prominent ridge 2-3 mm wide; breadth across anterior and posterior angles of zygomatic arches approximately equal, rather than anterior angle width distinctly greater; rostrum narrow, relative to length, rather than relatively short and broad; foramen rotundum relatively

low on alisphenoid, not obscured from view laterally by zygomatic arch, rather than relatively high on alisphenoid and obscured from lateral view by zygomatic arch. Baculum smallest for members of species group, proportions typical (Fig. 15; Table 8).

Specimens examined. — Arkansas: *Crawford Co.:* Fort Smith (3 USNM); *Ouachita Co.:* Camden (1 USNM); *Pulaski Co.:* 3 mi. E Wrightsville (1 SM); 2 mi. E Wrightsville (2 SM, 5 USNM); *Saline Co.:* Benton (2 USNM).

Oklahoma: *Adair Co.:* 2½ mi. E Stilwell (3 USNM); *Atoka Co.:* 5 mi. E Atoka (1 UMMZ); *Bryan Co.:* 4 mi. E Durant (2 OSU); *Carter Co.:* 2 mi. W Ratliff City (1 UMMZ); *Choctaw Co.:* 7 mi. SSE Fort Towson (4 SM); *Cleveland Co.:* Norman, Reeve's Park (1 SM); 1.6 mi. E Norman (1 SM); *Coal Co.:* 1 mi. W Coalgate (1 OSU, 1 UMMZ); *Creek Co.:* 15 mi. W Sapulpa (1 UIMNH); *Garvin Co.:* Washita River Bottom (1 OSU); *Grady Co.:* 1 mi. W Chickasha (1 OSU, 1 SM); *Haskell Co.:* Whitefield (1 OSU); *Hughes Co.:* Canadian River, S of Holdenville (1 OSU); *Lincoln Co.:* Chandler (2 UMMZ); *Love Co.:* 7 mi. S Marietta (1 UMMZ); *Marshall Co.:* 2 mi. E Willis (5 SM); 1 mi. W Willis (5 SM); S side Washita River on Hwy. 12 (1 UMMZ); Lake Texoma (1 UMMZ); *McClain Co.:* 2 mi. W Byars (1 OSU); Rosedale (1 OSU, 1 SM); *McIntosh Co.:* Eufaula (1 SM); *Muskogee Co.:* Wildlife Cons. Sta., Braggs (1 UMMZ); Ft. Gibson (1 UMMZ, 2 USNM); *Okfuskee Co.:* 3 mi. N, 1 mi. E Mason (1 OSU); *Oklahoma Co.:* 2 mi. E Tinker Field (1 OSU, 1 SM, 1 UMMZ); *Payne Co.:* Stillwater, Boomer Lake (1 OSU); 2 mi. S Stillwater (2 OSU); 5/10 mi. E Stillwater Cemetery (1 OSU); *Pittsburg Co.:* McAlester (2 OSU); *Pottawatomie Co.:* Asher (1 OSU, 1 UMMZ); *Pushmataha Co.:* Antlers (1 UMMZ); *Tulsa Co.:* 5 mi. W Sand Springs Bridge, Arkansas River (1 OSU); Mohawk Park (3 UMMZ); *Wagoner Co.:* Cowetta, S of Arkansas River (1 UMMZ).

Remarks.—*Geomys attwateri*, an additional species related to *G. breviceps*, occurs in south-central Texas, west of the Brazos River. See Honeycutt and Schmidly (1979) and Tucker and Schmidly (1981) for discussion.

Geomys lutescens Merriam, 1890
Yellow Pocket Gopher

Geomys lutescens lutescens Merriam, 1890

1890. *Geomys bursarius lutescens* Merriam, N. Amer. Fauna 4:51.

1895. *Geomys lutescens* Merriam, N. Amer. Fauna 8:127. First use of name combination.

1938. *Geomys lutescens hylaeus* Blossom, Occas. Papers Mus. Zool., Univ. Michigan 368:1. Type from 10 mi. S Chadron, Dawes County, Nebraska.

1940. *Geomys lutescens jugossicularis* Hooper, Occas. Papers Mus. Zool., Univ. Michigan 420:1. Type from Lamar, Prowers County, Colorado.

1940. *Geomys lutescens levisagittalis* Swenk, Missouri Valley Fauna 2:4. Type from Spencer, Boyd County, Nebraska.

1940. *Geomys lutescens vinaceus* Swenk, Missouri Valley Fauna 2:7. Type from Scottsbluff, Scotts Bluff County, Nebraska.

Type specimen.—USNM 23595, taken on 27 May 1889 from sandhills on Birdwood Creek, Lincoln County, Nebraska.

Distribution.—Widespread in western Nebraska and Kansas and adjacent parts of Colorado, South Dakota, and Wyoming in short-grass and mixed grass prairie (Fig. 1).

Description.—Size medium for genus; adult females averaging head and body length 162 mm to 182 mm, condylobasal length 39.4 mm to 43.3 mm (Fig. 3). Skull (Fig. 2C) broad and robust, dorsoventrally flattened; zygomata broad and roughly square in outline, broader anteriorly than posteriorly; temporal ridges separated by 2-3 mm; braincase short and broad; mastoid processes of moderate length, projecting at angle averaging 40°-50° from horizontal; posterior edge of premaxillary–frontal suture usually exceeding anterior edge of orbit; naso-frontal junction approximately flat in lateral view; foramen ro-

tundum relatively high on alisphenoid, usually obscured in lateral view by zygomatic arch. Incisors as in *G. bursarius*, but less procumbent. Anterior edge of P^4 usually straight in lateral profile; edge of P_4 usually convex. Molars as in *G. bursarius*.

Pelage color variable. Dorsal pelage usually with yellowish cast, especially on sides. A mid-dorsal stripe of dark fur, ranging from two to five cm wide present on most individuals. Dorsal color darkest and mid-dorsal stripe widest in north and east, especially north of Niobrara River, becoming more pallid to west; gophers from Wyoming and Colorado often sandy yellow. Localized regions with unusually dark or light soils often with similarly colored gophers (see Hendrickson, 1972, and "Nebraska region," below). "Peppering" due to black tips on dorsal hairs often present, though usually not conspicuous.

Diagnosis and comparisons.—Differs from all *G. bursarius* as noted in the discussion of *G. b. bursarius*. Differs from *G. l. major* in being slightly larger overall, maxillary usually not visible on sides of rostrum when viewed dorsally. Baculum moderate in length (mean = 10.8), unusually broad for species-group (Fig. 15; Table 8).

Specimens examined. — Colorado: *Adams Co.:* Barr (1 CSU); ¼ mi. W, 1 mi. E Bennett (11 KU); 5 mi. E Brighton (1 KU); 2 mi. E Brighton (6 KU); 6½ mi. N, 3 mi. W Strasburg (2 KU); 2 mi. N, 3¾ mi. W Strasburg (2 KU); *Bent Co.:* Las Animas (3 USNM); 4 mi. W Las Animas (3 MVZ); *Boulder Co.:* 8⅖ mi. E Boulder (1 KU); 1½ mi. S, 1 mi. E Lafayette (1 KU); *Douglas Co.:* 2 mi. N Parker (1 KU); *El Paso Co.:* 1½ mi. N, 9 mi. E Colorado Springs (1 CSU); Colorado Springs (1 KU); *Fremont Co.:* 4 mi. SSE Canon City (4 KU); *Larimer Co.:* 7 mi. NW Ft. Collins (1 CSU); 3⅘ mi. N Ft. Collins (1 CSU); 3 mi. N, 2 mi. W Ft. Collins (1 CU); 2½ mi. NE Ft. Collins (1 CSU, 1 CU); 2 mi. N Ft. Collins (1 CU); 2 mi. NW Ft. Collins (1 CSU); ½ mi. N Ft. Collins (1 CU); 3 mi. E Ft. Collins (2 CU); 2⅘ mi. E Ft. Collins (1 CU); Ft. Collins (1 CSU, 4 CU); 1 mi. S, 3½ mi. E Ft. Collins (1 CSU); 1 mi. N Laporte (1 CU); 1 mi. NE Masonville (1 CU); ½ mi. WSW Masonville (4 KU); *Logan Co.:* 1½ mi. S, 13 mi. W Peetz (1 KU); *Morgan Co.:* 2 mi. N, 2½ mi. W Ft. Morgan (5 KU); *Prowers Co.:* Lamar (1 UMMZ); 1 mi. S Lamar (1 CU, 1 UIMNH); *Washington Co.:* 9 mi. N, ½ mi. E Cope (1 KU); Cope (2 KU); ½ mi. S, 3 mi. W Cope (2 KU); ¾ mi. S, 1 mi. W Cope (2 KU); *Weld Co.:* ½ mi. N, 1 mi. W Briggsdale (1 KU); 5½ mi. E Ft. Lupton (1 KU); ¾ mi. N, 2¼ mi. E Hudson (1 KU); *Yuma Co.:* Wray (2 CU); 7 mi. S Wray (2 CU).

Kansas: *Barton Co.:* 8 mi. N Ellinwood (1 KU); *Cheyenne Co.:* 10 mi. N, 2 mi. W Bird City (2 MHP); 1 mi. N St. Francis (1 KU); 1 mi. W St. Francis (2 KU); 8 mi. S, 11½ mi. W St. Francis (1 KU); *Decatur Co.:* 1 mi. N, 1 mi. W Dresden (1 MHP); 1 mi. W Dresden (2 MHP); Oberlin (1 KU); *Ellis Co.:* ½ mi. N, 2 mi. E Ellis (3 MHP); 16 mi. N, 1 mi. W Hays (1 MHP); 1½ mi. N, 2 mi. W Hays (3 MHP); 1 mi. N, 2½ mi. W Hays (1 MHP); ½ mi. N, 3 mi. W Hays (1 MHP); ½ mi. N, 6 mi. W Hays (1 MHP); Hays (1 KU); 2 mi. W Hays (1 MHP); 6 mi. W Hays 1 (MHP); ¾ mi. W Yocemento (6 MHP); NE ¼ sec. 11, T15S, R20W (2 MHP); SW ¼ sec. 16, T15S, R19W (2 MHP); NE ¼ sec. 25, T13S, R19W (1 MHP); NW ¼ sec. 30, T13S, R18W (3 MHP); *Ellsworth Co.:* 2 mi. S Ellsworth (1 KU); *Finney Co.:* 3⅞ mi. N, ½ mi. W Garden City (1 KU); *Graham Co.:* 3¾ mi. N, 6 mi. E Hill City (3 MHP); 2 mi. N, 2½ mi. E Hill City (2 MHP); ½ mi. N, 5½ mi. E Hill City (1 MHP); *Greeley Co.:* 4¾ mi. E Tribune (1 KU); *Kearny Co.:* 10 mi. N Lakin (1 KU); 3½ mi. N, 4 mi. E Lakin (1 KU); 2¼ mi. W Lakin (2 KU); 15 mi. S, 4½ mi. E Leoti (1 KU); *Lane Co.:* Pendennis (2 KU); *Logan Co.:* 17⅞ mi. N Leoti (1 KU); *Ness Co.:* 1 mi. S, 16 mi. W Ness City (2 KU); *Norton Co.:* ¾ mi. N, 4 mi.

E Lenora (3 MHP); Norton (1 MHP); 3 mi. S Norton (2 KU); 4 mi. S, 4 mi. W Norton (1 MHP); *Osborne Co.:* ½ mi. E Alton (2 KU); ½ mi. S, 1½ mi. E Alton (1 KU); ½ mi. S, 1 mi. E Alton (1 KU); ½ mi. S, ½ mi. E Alton (2 KU); *Phillips Co.:* 1 mi. S, 2 mi. W Glade (1 MHP); ¼ mi. N, 7 mi. W Kirwin (1 MHP); 6 mi. W Kirwin (1 MHP); ½ mi. S, 6 mi. W Kirwin (1 MHP); *Rawlins Co.:* 2 mi. E Atwood (1 KU); S bank Lake Atwood (1 MHP); ½ mi. N, 3 mi. E Herndon (5 MHP); *Rooks Co.:* 4 mi. N, 2⁷⁄₁₀ mi. E Damar (2 MHP); ¼ mi. S, 6 mi. E Stockton (5 KU); 1 mi. S, 8 mi. W Stockton (3 KU); *Russell Co.:* 7 mi. S, 1 mi. E Lucas (3 KU); W ½ sec. 9, T13S, R11W (1 MHP); E ½ sec. 10, T13S, R11W (1 MHP); *Sherman Co.:* 15 mi. N, 3 mi. E Edson (15 KU); *Thomas Co.:* 7 mi. N, 2½ mi. E Colby (7 KU); *Trego Co.:* 15 mi. N, 2 mi. E Brownell (6 MHP); 8½ mi. N Ogallah (1 MHP); 11 mi. S, 2 mi. W Ogallah (1 MHP); 4 mi. N, 1 mi. E WaKeeney (1 MHP); *Wallace Co.:* 10½ mi. N, 4½ mi. W Weskan (1 MHP); 5¾ mi. N, 1½ mi. W Weskan (3 MHP); 5¼ mi. N Weskan (1 MHP); 1½ mi. N Weskan (1 MHP); *Wichita Co.:* 1⁹⁄₁₀ mi. S Leoti (1 KU); 15 mi. W Scott City (1 KU); 17 mi. W Scott City (1 KU).

Nebraska: *Antelope Co.:* 7 mi. W Clearwater (5 NSM); 2¼ mi. N, 7 mi. W Elgin (1 FMNH, 2 UMMZ); 6¼ mi. N, 1 mi. E Neligh (1 KU); 5½ mi. N Neligh (1 SM); 4 mi. N Neligh (1 SM); Neligh (1 NSM, 3 SM, 3 USNM); ½ mi. S, ½ mi. W Neligh (1 KU); 1 mi. SW Neligh (1 KU); 1½ mi. S Neligh (2 SM); 2 mi. S, 1 mi. W Neligh (4 KU); 4 mi. S Neligh (2 SM); 4½ mi. S Neligh (1 SM); 5 mi. S, 1 mi. E Neligh (1 SM); ⁷⁄₁₀ mi. N, 1 mi. W Oakdale (5 KU); ⅒ mi. N, 1 mi. W Oakdale (2 FMNH); ⅒ mi. N, 1⅒ mi. W Oakdale (1 KU); ⅒ mi. N, 1⁷⁄₁₀ mi. W Oakdale (2 KU, 1 UMMZ); ⁹⁄₁₀ mi. W Oakdale (1 UMMZ); 1⅒ mi. W Oakdale (1 KU); 1⁷⁄₁₀ mi. W Oakdale (2 UMMZ); 1⅒ mi. W Oakdale (9 KU); 1½ mi. W Oakdale (1 SM); 2 mi. W Oakdale (1 SM); ⅒ mi. S, 1 mi. W Oakdale (2 FMNH, 2 UMMZ); ⅒ mi. S, 1⁷⁄₁₀ mi. W Oakdale (3 KU, 1 UMMZ); ⁷⁄₁₀ mi. S, 1 mi. W Oakdale (1 FMNH, 1 KU); ⁷⁄₁₀ mi. S, 1⁷⁄₁₀ mi. W Oakdale (1 UMMZ); ½ mi. S, 3 mi. W Oakdale (2 FMNH, 1 UMMZ); ½ mi. S, 3½ mi. W Oakdale (2 FMNH); ½ mi. S, 3¾ mi. W Oakdale (1 FMNH, 1 UMMZ); (vicinity of) Oakdale (1 USNM). *Banner Co.:* 10 mi. S, 2½ mi. E Gering (4 KSC); no specific locality (1 NSM); *Boyd Co.:* 1 mi. W Bristow (2 KU); 1½ mi. W Bristow (1 KU); 2 mi. S, ½ mi. W Butte (1 KU); 5 mi. WNW Spencer (1 KU); 2 mi. N Spencer (2 KU); 1 mi. WNW Spencer (4 KU); ½ mi. N Spencer (2 KU); *Brown Co.:* 11¾ mi. N, 6 mi. E Ainsworth (1 KU); 12 mi. N Johnstown (1 KU); 7 mi. N Johnstown (1 KU); 6½ mi. N Johnstown (2 KU); 2½ mi. N, ½ mi. E Long Pine (2 KSC); 1½ mi. S Long Pine (6 KU); 23 mi. S Long Pine (1 KSC); *Buffalo Co.:* 3 mi. N Kearney (1 KSC); 2 mi. S, 2 mi. E Kearney (1 KSC); 3 mi. S, 5 mi. W Kearney (1 KSC); *Cherry Co.:* Hackberry Lake (3 KU); 10 mi. S Nenzel (1 KSC); 4 mi. E Valentine (1 KU); Valentine (1 NSM); 15 mi. S, 3 mi. W Valentine (2 UIMNH); 15 mi. S, 4 mi. W Valentine (1 UIMNH); 23 mi. S, 6 mi. W Valentine (3 UIMNH); 23 mi. S, 9 mi. W Valentine (3 UIMNH); Niobrara Wildlife Refuge (3 NSM); *Cheyenne Co.:* 2 mi. N Dalton (1 KU); Dalton (1 NSM); 15 mi. S Dalton (5 KU); Lodgepole (1 NSM); Sidney (2 NSM); *Custer Co.:* 18 mi. S Ansley (1 KSC); 18 mi. S, 3 mi. W Ansley (1 KSC); 1 mi. S, 2 mi. W Broken Bow (3 KSC); 23 mi. S, 5 mi. E Broken Bow (1 KSC); 4 mi. N, 3 mi. E Oconto (1 KSC); *Dawes Co.:* Chadron (1 NSM); 10 mi. S Chadron (2 KU, 4 UMMZ); 13 mi. S, 3 mi. E Chadron (3 KU, 44 NSM); 5½ mi. S Crawford (3 KSC); *Dawson Co.:* Lexington (1 NSM); *Deuel Co.:* Chappell (1 NSM); 4 mi. W Chappell (3 KSC); *Dundy Co.:* 2 mi. SW Benkelman (1 KU); 5 mi. N, 2 mi. W Parks (6 KU); 4 mi. N, 1½ mi. W Parks (1 MHP); *Franklin Co.:* 1 mi. SW Franklin (8 KU); *Greeley Co.:* 10 mi.

N Greeley (1 KSC); *Harlan Co.:* 1 mi. S, 2 mi. W Alma (3 KSC); *Hitchcock Co.:* 10 mi. S, 2 mi. E Stratton (1 NSM); Trenton (1 KU); *Holt Co.:* 6 mi. S, ½ mi. W Butte (2 KU); 6 mi. N Midway (4 KU); 24 mi. N O'Neill (1 KU); 23½ mi. N O'Neill (2 KU); *Kearney Co.:* 1 mi. S, 8 mi. E Kearney (1 KSC); 3¾ mi. S Kearney (2 KU); 4 mi. S, 4 mi. E Kearney (3 KSC); 4 mi. S, ¼ mi. E Kearney (2 KSC); *Keith Co.:* 4 mi. WNW Keystone (1 KU); no specific locality (1 NSM); *Keya Paha Co.:* ½ mi. N, ½ mi. W Norden (2 KU); Norden (1 KU); 12 mi. N Springview (2 KU); 10 mi. N Springview (1 KU); 4 mi. S Springview (3 KU); *Kimball Co.:* Kimball (3 NSM); *Lincoln Co.:* Brady (1 NSM); 1 mi. W Brady (11 KSC); 8 mi. N, 4 mi. W Hershey (8 KU); 7 mi. N, 4 mi. W Hershey (2 KU); 6 mi. N, 2 mi. E Sutherland (1 KU); 2 mi. N, 1 mi. E Sutherland (2 KU); 4 mi. S, 2 mi. W Sutherland (2 KU); 7 mi. S, 1 mi. W Sutherland (1 KU); *McPherson Co.:* 25 mi. N North Platte (2 NSM); *Morrill Co.:* Bridgeport (1 NSM); *Rock Co.:* 8½ mi. N, 2½ mi. W Bassett (1 KSC); 4½ mi. N Bassett (1 KU); 3½ mi. N Bassett (3 KU); 1½ mi. W Bassett (1 KSC); 2½ mi. S, 4 mi. W Bassett (2 KU); *Scotts Bluff Co.:* Scottsbluff (2 NSM); 1 mi. E Scottsbluff (3 KU); 2 mi. S, 1 mi. W Scottsbluff (2 KU); 12 mi. S Scottsbluff (2 KU); *Sheridan Co.:* NW side Snow Valley, N Lakeside (1 NSM); *Sioux Co.:* 3 mi. E Agate (1 KU); 6½ mi. W Crawford (4 NSM); 1 mi. S, 4 mi. W Crawford (2 NSM); Glen (1 NSM); 8 mi. N Harrison (1 UMMZ); 5 mi. N, 2½ mi. W Harrison (1 KSC); Harrison (1 NSM); *Thomas Co.:* 3 mi. S, 6 mi. W Halsey (1 KSC); *Valley Co.:* 4 mi. N, 2 mi. W Arcadia (2 KSC); 2½ mi. N, ½ mi. W Elyria (3 KSC); *Webster Co.:* ½ mi. S, 3 mi. W Red Cloud (1 KSC); *Wheeler Co.:* 1 mi. S Ericson (1 KSC).

South Dakota: *Bennett Co.:* La-Creek Nat. Wildlife Refuge (1 MHP); 4 mi. S, 8 mi. E Martin (1 KU); 7 mi. S, 4 mi. E Martin (1 MHP); 8 mi. S Martin (3 KU); 10 mi. S Martin (1 KU); *Fall River Co.:* 1 mi. E Edgemont (2 KU); *Jackson Co.:* 2 mi. S, 2 mi. E Interior (1 KU); *Todd Co.:* 2 mi. N, 3 mi. W Rosebud (2 KU); *Washabaugh Co.:* 10 mi. N, 4 mi. E Potato Creek (2 KU).

Wyoming: *Converse Co.:* 3 mi. N, 5 mi. E Orin (3 KU); *Goshen Co.:* 8 mi. SSE Torrington (1 KU); *Laramie Co.:* 1 mi. W Gallio (1 KU); 6 mi. W Meriden (2 KU); 6½ mi. W Meriden (13 KU); 2½ mi. SW Meriden (1 KU); *Niobrara Co.:* 10 mi. N Hat Creek (16 KU); 2 mi. S, ½ mi. E Lusk (2 KU); *Platte Co.:* 3 mi. W Guernsey (1 KU); *Weston Co.:* 23 mi. SW Newcastle (4 KU).

Geomys lutescens major Davis, 1940

1940. *Geomys lutescens major* Davis, Texas Agr. Exp. Sta. Bull. 590:32.

1947. *Geomys bursarius industrius* Villa-R. and Hall, Univ. Kansas Publ., Mus. Nat. Hist. 1:226. Type from 1½ mi. N Fowler, Meade County, Kansas.

Type specimen.—Texas Cooperative Wildlife Collection (Texas A&M University) 819, obtained 29 December 1938 at 8 mi. W Clarendon, Donley County, Texas.

Distribution.—Occurs in southeastern Colorado, southwestern Kansas, western Oklahoma, east-central New Mexico, and northwestern Texas in short-grass prairie and mesquite prairie and in southeastern Missouri in tall-grass prairie/deciduous forest mosaic (Fig. 1; see also Honeycutt and Schmidly, 1979).

Diagnosis and comparisons.—Differs from *G. bursarius* as discussed above. Differs from *G. l. lutescens* in being smaller on average, and having proportionately shorter skulls and narrower zygomatic arches, but greater mastoid breadth; frontal-premaxillary suture on dorsum of skull falling posterior to anterior edge of orbits; maxillary usually visible on sides of rostrum when viewed dorsally (Fig. 2D). Color extremely variable, generally dark brown in east and pale yellow-brown in west, but irregular in geographic pattern. Dorsal stripe of darkened fur sometimes present, but rarely conspicuous to the degree seen

in *G. l. lutescens*. Baculum long (mean = 11.2 mm) but narrow distally (Fig. 15; Table 8).

Specimens examined.—KANSAS: *Barber Co.:* 2 mi. E Aetna (1 MHP); Aetna (1 MHP); 1 mi. W Aetna (1 KU); 1 mi. S Aetna (1 KU); 1 mi. N, 19½ mi. E Coldwater (1 KU); 8 mi. N, 2 mi. E Hardtner (3 MHP); 5 mi. N, 4½ mi. E Hardtner (1 MHP); 7 mi. N, 7 mi. W Kiowa (1 KU); 6 mi. NW Medicine Lodge (1 KU); 2 mi. W Medicine Lodge (1 KU); ¼ mi. S, 1 mi. W Medicine Lodge (1 MHP); ¾ mi. S, 1 mi. W Medicine Lodge (1 MHP); 1 mi. S, 1 mi. W Medicine Lodge (2 MHP); 1¾ mi. S, 1 mi. W Medicine Lodge (1 MHP); 2 mi. S, 1 mi. W Medicine Lodge (2 MHP); 3¼ mi. S Medicine Lodge (1 MHP); 3 mi. N, 1¼ mi. E Sharon (2 MHP); 2½ mi. N, 1½ mi. E Sharon (1 KU); Sharon (1 KU); 2½ mi. S Sun City (1 KU); 3 mi. S Sun City (1 KU); 4½ mi. S Sun City (1 KU); *Clark Co.:* 3⁷⁄₁₀ mi. N, 12 mi. W Ashland (1 KU); 1 mi. N, 12 mi. W Ashland (1 KU); 12 mi. E Ashland (1 KU); ½ mi. E Ashland (1 KU); 1⁷⁄₁₀ mi. W Ashland (1 KU); 5⁷⁄₁₀ mi. W Ashland (1 KU); 6 mi. S Kingsdown (1 KU); 7 mi. SW Kingsdown (1 KU); *Comanche Co.:* 1 mi. N, 15½ mi. E Coldwater (2 KU); 1 mi. N, 14¾ mi. E Coldwater (1 KU); 5 mi. S, 11 mi. W Coldwater (1 KU); 10½ mi. S Protection (1 MHP); *Cowley Co.:* 3 mi. SE Arkansas City (2 KU); *Edwards Co.:* 1 mi. N Kinsley (1 MHP); Kinsley (1 SM); 3 mi. E Offerle (1 MHP); *Finney Co.:* 2 mi. S Garden City (1 KU); 4¹⁄₁₀ mi. S Garden City (2 KU); 6½ mi. S Garden City (1 KU); 1 mi. S Pierceville (2 KU); *Ford Co.:* 2 mi. SW Dodge City (6 KU); 3⅘ mi. SW Dodge City (1 KU); 10 mi. N, 4½ mi. W Mullinville (1 MHP); *Gray Co.:* 1 mi. S Cimarron (1 KU); 2 mi. S Cimarron (1 KU); 2½ mi. S Cimarron (2 KU); 4½ mi. S Cimarron (1 KU); 5⅘ mi. S Cimarron (1 KU); 6 mi. S Cimarron (2 KU); 6¹⁄₁₀ mi. S Cimarron (1 KU); 7⅗ mi. S Cimarron (1 KU); 7⅘ mi. S Cimarron (1 KU); *Hamilton Co.:* 1 mi. E Coolidge (4 KU); 1 mi. S Coolidge (3 MHP); 2⅛ mi. N, ½ mi. W Syracuse (3 KU); 1½ mi. N, ½ mi. W Syracuse (1 KU); *Harper Co.:* 1 mi. N, ½ mi. E Corwin (1 MHP); 1¼ mi. S, 1½ mi. E Corwin (2 MHP); 4½ mi. N Danville (2 KU); 1 mi. N Harper (2 KU, 1 UIMNH); *Harvey Co.:* Halstead (1 KU); 1¼ mi. N, 13¼ mi. W Newton (2 KU); *Kearny Co.:* 2⅘ mi. E Lakin (1 KU); 2⁷⁄₁₀ mi. E Lakin (1 KU); 1⅘ mi. E Lakin (1 KU); 4 mi. S Lakin (1 KU); *Kiowa Co.:* 5 mi. N Belvedere (1 KU); 1½ mi. S, 3½ mi. E Belvedere (2 MHP); Greensburg (1 MHP); 7¾ mi. S, 4 mi. E Haviland (1 MHP); *Meade Co.:* 3½ mi. NE Fowler (1 KU); 2 mi. N Fowler (1 KU); 1½ mi. N Fowler (1 UMMZ); 7 mi. N Meade (1 KU); 8 mi. S, 2 mi. W Meade (1 MHP); 13 mi. SW Meade (6 KU); Meade County State Park (4 KU, 1 UMMZ); *Morton Co.:* 12 mi. N Elkhart (1 KU); 7½ mi. N, 1½ mi. W Elkhart (1 KU, 2 MHP); 7 mi. N Elkhart (1 MHP); 1⅘ mi. N Elkhart (2 KU); 7½ mi. S Richfield (1 KU); no precise locality (1 KU); *Pawnee Co.:* 3⁹⁄₁₀ mi. NE Larned (2 KU); Larned (1 KU); 1 mi. S, 1 mi. E Larned (2 KU); *Pratt Co.:* Pratt (3 KU); *Reno Co.:* ½ mi. E Hutchinson (1 MHP); *Rice Co.:* ½ mi. N, 12 mi. E Sterling (3 MHP); *Seward Co.:* 10½ mi. N Liberal (1 SM); 6 mi. N, 8 mi. E Liberal (1 KU); 3 mi. N, 4 mi. E Liberal (2 KU); 1 mi. S, 1 mi. W Liberal (1 KU); *Stanton Co.:* 1 mi. N, 6 mi. W Manter (1 KU); *Stafford Co.:* Little Salt Marsh (1 KU).

MISSOURI: *Carter Co.:* Hunter (4 USNM); *Wayne Co.:* Willamsville (8 USNM).

OKLAHOMA: *Alfalfa Co.:* 3 mi. N, 6½ mi. E Cherokee (1 SM); Cherokee (1 OSU, 1 UMMZ); Great Salt Plains Wildlife Ref. (2 OSU); *Beaver Co.:* 2 mi. W Forgan (1 UMMZ); *Beckham Co.:* ½ mi. S Sayre (1 OSU); *Blaine Co.:* Canton Shooting Grounds (1 OSU); Roman Nose State Park (1 OSU); Watonga (1 OSU); *Caddo Co.:* 5 mi. W Cogar (1 USNM); 1 mi. S Hinton (4

SM); 2 mi. N Hinton (1 OSU); *Canadian Co.:* 2 mi. S, 4 mi. E Union City (1 OSU); *Cimarron Co.:* 8 mi. W Boise City (2 OSU, 3 UMMZ); Cimarron River, N of Boise City (1 OSU); *Cleveland Co.:* 3 mi. N Lexington (2 SM); 1⅝ mi. N Norman (1 SM); 1½ mi. E Norman (1 SM); Norman (1 OSU); Norman, Univ. Oklahoma campus (1 SM); Norman, Reeve's Park (1 SM); Norman, intersection Timberdell and Asp (2 SM); ½ mi. S Norman (2 USNM); 1 mi. S Norman (1 SM); 2¼ mi. S Norman (1 SM); 3 mi. SW Norman (2 USNM); 2 mi. S Slaughterville (2 SM); *Comanche Co.:* Lawton (2 USNM); *Cotton Co.:* 5 mi. SE Taylor (1 SM); 8 mi. E Walters (1 UMMZ); *Custer Co.:* Weatherford (2 KU); *Dewey Co.:* 5 mi. W Canton (1 KU); 5 mi. SE Vici (1 OSU); *Ellis Co.:* Shattuck (3 UMMZ); *Garfield Co.:* 8 mi. W Enid (1 OSU); *Grady Co.:* ⅒ mi. S, 3 mi. W Blanchard (1 SM); *Grant Co.:* 1 mi. N, 1⅒ mi. W Hawley (2 SM); *Harmon Co.:* 1 mi. SW Hollis (1 UMMZ); *Harper Co.:* USDA Southern Plains Exp. Range Sta. (4 OSU, 4 UMMZ); Buffalo Creek on Hwy. 64 (1 OSU); 10 mi. W Buffalo (2 OSU, 1 UMMZ); 5 mi. N Fort Supply (1 USNM); 3 mi. N Fort Supply (1 USNM); *Jackson Co.:* 5 mi. SW Eldorado (1 UIMNH); *Jefferson Co.:* 1 mi. E Ringling (2 UMMZ); *Kay Co.:* Ponca Agency (3 MSU); 2½ mi. S, 10 mi. W Tonkawa (1 OSU); SE ¼ sec. 18, T26N, R2E (1 OSU); *Major Co.:* 5½ mi. S Waynoka (1 SM); *McClain Co.:* 1 mi. S, 1 mi. W Norman (1 SM); Wayne (2 OSU, 1 SM); *Oklahoma Co.:* Oklahoma City (3 KU); *Pawnee Co.:* ½ mi. W Cleveland (1 OSU); *Payne Co.:* ½ mi. S, 5 mi. W Stillwater (1 OSU); 4½ mi. W Stillwater (1 OSU); 1½ mi. SW Stillwater (1 OSU); 2 mi. S, 1 mi. W Stillwater (1 OSU); *Pottawatomie Co.:* 1 mi. W Tecumseh (1 SM); *Roger Mills Co.:* 1⁷⁄₁₀ mi. N Cheyenne (1 SM); 1 mi. N Cheyenne (1 OSU); *Stephens Co.:* ¼ mi. E Claude (1 SM); 1 mi. S, ¼ mi. E Claude (1 SM); 1 mi. E Marlow (2 OSU, 1 SM, 1 UMMZ); *Texas Co.:* Guymon (1 OSU, 1 UMMZ); *Tillman Co.:* Frederick Cemetery (1 UMMZ); *Woods Co.:* Waynoka (1 UMMZ); 5 mi. S Waynoka (1 SM); 12 mi. N Alva (1 OSU); Alva (1 USNM); 3 mi. E Camp Houston (1 OSU); E side Cimarron River on Hwy. 64 (1 UMMZ); *Washita Co.:* 4 mi. E Cordell (1 UMMZ); *Woodward Co.:* 2 mi. NNE Woodward (1 SM); 2 mi. NNW Woodward (1 SM); 3½ mi. WNW Woodward (1 SM); Woodward (1 USNM).

Remarks.—In addition to the two subspecies of *G. lutescens* found in our study area, there are three other taxa which must be considered. The form named *knoxjonesi* by Baker and Genoways (1975) is similar to *G. l. major* in cranial morphology, karyology (Honeycutt and Schmidly, 1979), and ectoparasites (Timm and Price, 1980) and we consider it to be a subspecies of *G. lutescens.* The status of *llanensis* and *texensis*, which are isolated populations on the Edwards Plateau of central Texas, is less certain. They are karyotypically very similar to *G. l. knoxjonesi*, but are distinct cranially, and have ectoparasites more allied with *G. breviceps.* Until additional studies are carried out, we suggest that they be tentatively listed as subspecies of *Geomys lutescens.*

RESULTS AND DISCUSSION

SIZE VARIATION

Geographic variation in size is shown in Fig. 3; mean condylobasal length of adult females was used in each OTU as our estimator of size. The largest *Geomys* occur in northeastern Iowa, with size decreasing radially in all directions; the smallest pocket gophers in our study area occur in south-central Nebraska and in southeastern Oklahoma. The figure shows that, although most size variation is clinal, there is a geographically con-

tinuous discontinuity in the cline in eastern Nebraska and Kansas. In this region there is an abrupt change from less than 44 mm to greater than 46 mm; only a single population in southeastern Kansas is intermediate. Single specimens that were not included in the OTU means indicate that the clinal discontinuity is clearly no more than 30 km wide, and is narrower in many places. The detailed nature of the discontinuity has been studied in two areas. In Antelope County, Nebraska, the change in size is extremely abrupt, with a change from 42 mm to 47 mm taking place over a distance of about 2 km (Heaney, 1979, and data reported below). In northeastern Kansas, the width is less certain, but is less than 30 km and perhaps as little as 10 km (Hendrickson, 1972). In both of these areas, and apparently throughout the region of the size discontinuity, there is an abrupt change in dominant vegetation from tall-grass

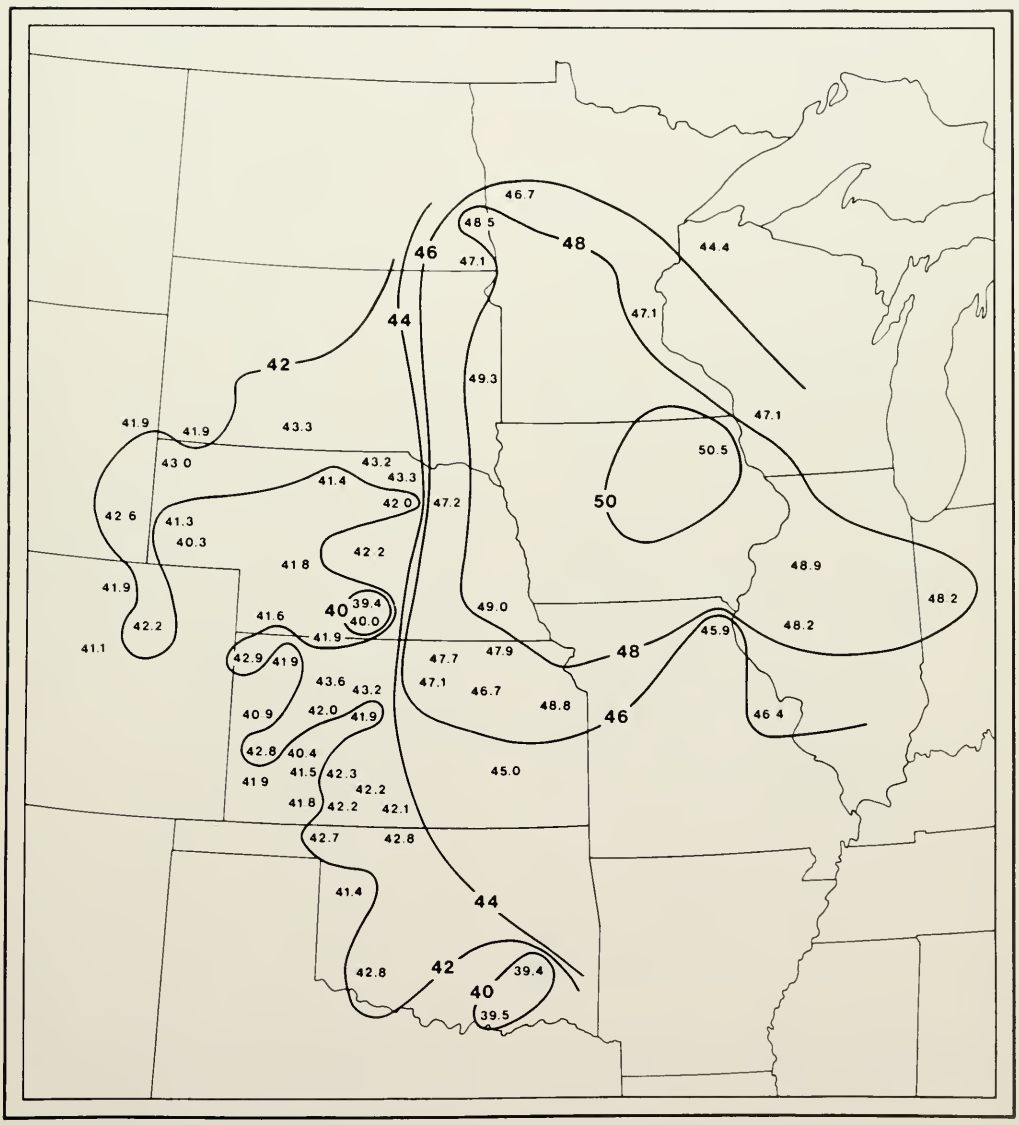

FIG. 3.—Map of the central and northern Great Plains showing geographic variation in mean condylobasal length (in mm) of adult female *Geomys;* scale as in Fig. 1.

prairie to the east, and short- or mid-grass prairie to the west, with a parallel change from dark silt-loam soils to light sandy loams, as discussed below.

CLUSTER ANALYSIS OF OTUS

An initial assessment of multivariate geographic patterns in similarity of the gophers was conducted by cluster analysis of the OTUs that contained five or more individuals (see Methods). The resulting phenogram was then used to group taxa into three levels of similarity; the "similarity isoclines" are shown in Fig. 4. Two major groups are apparent. In the eastern group, which corresponds to the species *G. bursarius*, the most distinct subgroups are the subspecies *G. b. illinoensis* and *G. b. wisconsinensis;* a population in eastern Iowa is less dis-

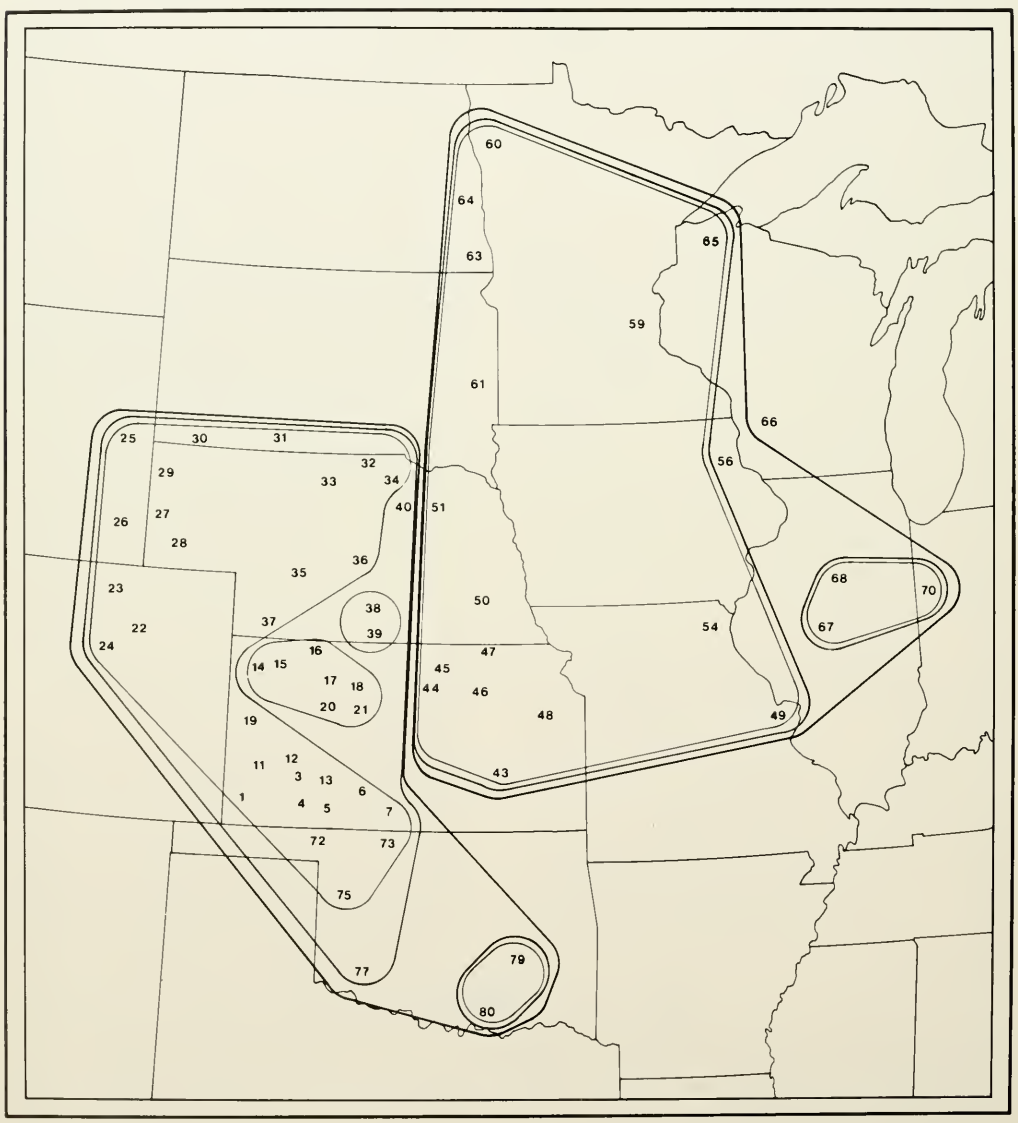

Fig. 4.—Map of the central and northern Great Plains showing levels of similarity of OTUs of adult female *Geomys* based on cluster analysis; scale as in Fig. 1. For locations of numbered localities, see "Methods and Materials."

tinct. There is no tendency for the remaining populations to cluster into northern and southern groups as would be expected if the gophers in this region should be divided into two subspecies (*G. b. bursarius* and *G. b. majusculus*), as has often been done (e.g., Villa-R. and Hall, 1947; Jones, 1964; Bowles, 1975; Hall, 1981).

The western group corresponds to the species *G. lutescens* and *G. breviceps* as defined in this study. The "similarity isoclines" show the populations of *G. lutescens* to be fairly homogeneous; the gophers from southwestern Kansas and adjacent Oklahoma *(G. l. major)* did not form a distinct group in the analysis. *Geomys breviceps* was clearly most similar to *G. lutescens,* but was distinct at all but the highest levels of clustering.

DISCRIMINANT FUNCTION ANALYSES

These analyses were first carried out to test the null hypothesis of no difference between a large number of OTUs, all of which were considered simultaneously. In the initial analyses, all OTUs having five or more specimens were considered as distinct groups and differences were sought. For convenience, analyses were done on four geographic units; these were 1) Colorado, Kansas, and Missouri; 2) Nebraska, southern South Dakota, and Wyoming; 3) Illinois, Indiana, Iowa, Minnesota, Missouri, North Dakota, eastern South Dakota, eastern Nebraska, and eastern Kansas; and 4) Arkansas, Missouri, and Oklahoma.

Kansas region.—Analysis of the first region indicated that all OTUs from southwestern Kansas overlapped greatly and were not distinguishable from one another (Fig. 5). These populations had previously been divided into three subspecies (*industrius, jugossicularis,* and *major*) (Villa-R. and Hall, 1947), but they all may be referred to *G. l. major* (see below). They were distinct from most, but not all, northwestern Kansas OTUs, and were highly distinct from all groups from northeastern Kansas and Missouri. The northwestern OTUs, which overlapped greatly among themselves (Fig. 5), are not distinguishable from gophers from western Nebraska (see below), and are considered to be *G. l. lutescens.* The OTU from east-central Missouri was not distinguishable from eastern Kansas OTUs, but was distinguishable from all others. The eastern OTUs in Kansas were highly distinct from the two western groups; the eastern group, and also the Missouri OTU, are part of *G. bursarius* as defined here.

In the second Kansas region analysis, small samples and specimens from the areas of contact between the taxa were entered into the analysis as unknowns, and compared with the aggregated samples of *G. b. bursarius, G. l. lutescens,* and *G. l. major.* The specimens from Colorado identified as *G. l. lutescens* also were used as a group of "knowns," as was the sample of gophers from eastern Missouri. The Missouri sample was not significantly different from the Kansas *G. bursarius* sample ($F = 1.49$, $p > .05$), but all other groups entered as known could be significantly distinguished. However, 21 of 100 *G. l. lutescens* from Kansas were misclassified with the Colorado group, and eight of 50 from Colorado were misclassified as being from Kansas, thus indicating their high level of similarity.

Villa-R. and Hall (1947:231) stated that it was the ". . . intermediate nature of . . . specimens from Butler County and . . . McPherson County, Kansas, that have caused us to treat *G. b[ursarius] majusculus* . . . as only subspecifically distinct from the more western subspecies, *[G. lutescens] major* . . . ." One Butler County and all but one McPherson County specimens were juveniles, and so not usable by us. The remaining two specimens were entered into our analysis as unknowns, and were assigned to *G. bursarius* with posterior probabilities in excess of .95; they also had all qualitative cranial characters associated with *G. bursarius,* and we con-

sider them to be typical representatives of that species.

Hendrickson (1972) suggested that specimens from the vicinity of Osborne County, Kansas, represent intergrades between *lutescens* and *bursarius*. We entered three females from western Osborne County, two from eastern Osborne County, one from Jewell County, and two from eastern Russell County as unknowns in the second analysis. Specimens from western Osborne and Russell counties were identified as *G. lutescens* with posterior probabilities in excess of .95. Those from eastern Osborne County and Jewell County were identified as *G. bursarius* with posterior probabilities of .92, .95, and 1.00, respectively. Males from eastern Jewell and western Osborne counties were included in an analysis conducted in the same fashion using adult males. The one male from Jewell County was assigned to *G. bursarius* with a .99 probability, and the three from western Osborne County were assigned to *G. lutescens* with probabilities in excess of .95.

Additionally, we entered females from Barton (1), Ellsworth (1), Rice (1), Pratt (2), and Cowley (3) counties as unknowns; all but the one from Rice County were assigned to *G. lutescens* with probabilities in excess of .95; the one from Rice County had a probability of .81. Males from Stafford (1), Barton (1), Harvey (2), Rice (2), Reno (1), Harper (3), and Cowley (1), were analyzed similarly and were all identified as *G. lutescens* with posterior probabilities in excess of .95.

The cluster analysis and discriminant function analyses discussed above indi-

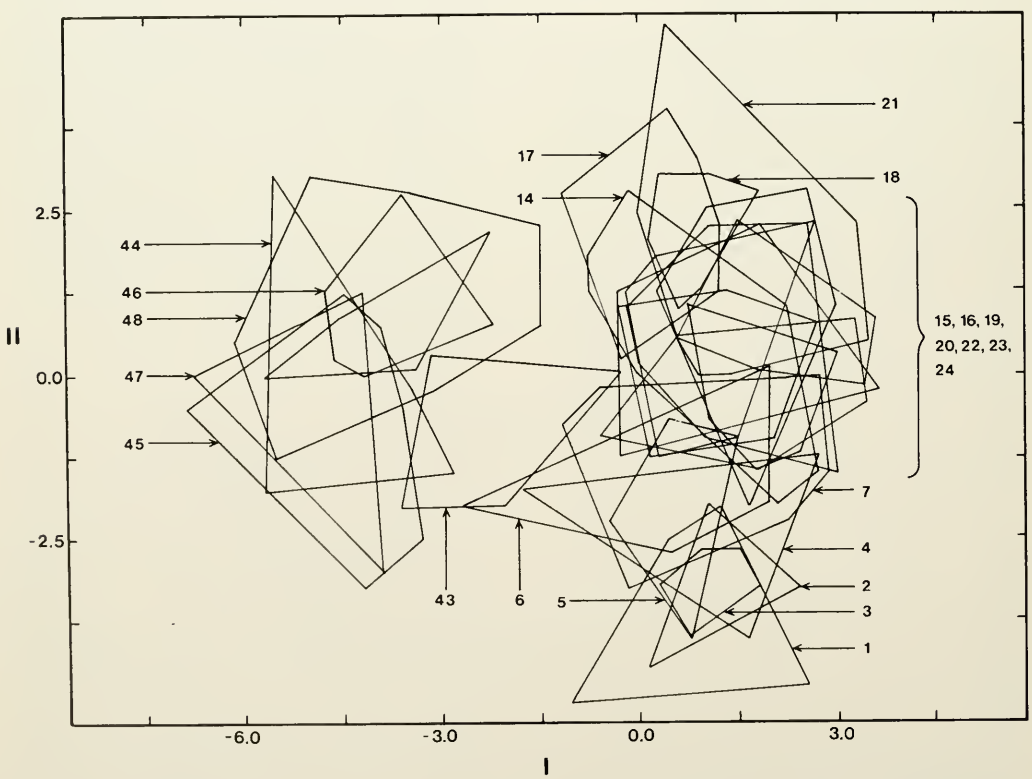

Fig. 5.—Graph of the first two axes of the discriminant function analysis of the Kansas region OTUs. Polygons on the left are *G. bursarius*, in the upper right are *G. l. lutescens*, and in the lower right are *G. l. major*. Numbers correspond to OTU numbers; see text.

cated that gophers in the species *G. lutescens* fall into two groups for which the names *lutescens* and *major* are available. In order to test for evidence of intergradation between the two taxa, we entered all gophers from the area of contact (as defined by Villa-R. and Hall, 1947, and the results of our cluster analysis shown in Fig. 4) as unknowns in the second-level discriminant function analysis described above. The results indicated that gophers from the floodplain of the Arkansas River in Kearny and Finney counties in west-central Kansas and in Barton, Cowley, Harper, Harvey, and Rice counties in south-central Kansas (a zone 40-50 km wide) showed indications of intergradation between *lutescens* and *major,* and it is on this basis that we consider them to be conspecific. The assignment of a small number of these individuals is arbitrary in that the probability of belonging to either taxon is roughly equal (e.g., specimens from Barton and Harvey counties), and in some cases individuals from the same locality (e.g., specimens from Hamilton and Harper counties) could be assigned to different subspecies. We interpret this as evidence of a fusion type of hybrid zone (Heaney, 1979) in which selection for the two genomes has occurred at different intensities in different localities. It would appear that part of the *lutescens* genome extends into southern Kansas from Barton through Harper counties, but because the majority of individuals are most similar to *major,* we have assigned all specimens to that taxon.

The subspecies *G. l. jugossicularis* was named on the basis of two specimens from Lamar, Prowers County, Colorado (Hooper, 1940); nine specimens from Morton County, Kansas, were also referred to that subspecies by Hooper. The Morton County specimens were entered into the first discriminant function analysis as knowns in a single OTU; in that analysis, all were nearly identical to those gophers to the east which had been included in the subspecies *major* and *industrius.* The paratype, an adult female, and a young adult female from 1 mi. S Lamar were entered into the second-level discriminant function analysis as unknowns. They were both assigned to *G. l. lutescens* with posterior probabilities of .767 and .749, respectively. Two females from 4 mi. W Las Animas, Bent County, Colorado, were also assigned to *G. l. lutescens* with probabilities in excess of .85. Although few specimens are available from southeastern Colorado, it appears that *G. l. lutescens* extends south at least as far as Lamar and Las Animas in Colorado. In spite of evidence that some intergradation does occur in the area (e.g., the specimen from El Paso County, which had a posterior probability of .691 of belonging with *G. l. major,* and the two from 1 mi. S Lamar), and in spite of the fact that most of the specimens referred to this taxon in the past are consubspecific with those in southwestern Kansas, the name *jugossicularis* must be regarded as a junior synonym of *G. l. lutescens* because specimens from the type locality are most similar to that taxon.

As noted by McLaughlin (1958), the populations he named as *G. b. missouriensis* represent a zoogeographic enigma. One of the two known main populations occurs primarily on the floodplain and river bluffs of the Missouri River near its confluence with the Mississippi River. The other population occurred along a single railroad right-of-way in the Ozark uplands of Carter and Wayne counties in southeastern Missouri; McLaughlin searched for them there 60 years after their discovery, and concluded that they were extinct. Although *G. b. illinoensis* occurs across the Mississippi River immediately to the east of the St. Louis area, we suspect that the river forms a very rarely crossed barrier because we found no evidence of interbreeding between the two taxa. The St. Louis area population is about 150 km from the nearest known population of *G. b. bursarius.* The southern population was about 120 km from the

St. Louis gophers (although new specimens from Crawford and Perry counties narrow this apparent gap), 175 km from the nearest known population of *G. breviceps sagittalis* in Arkansas, and 200 km from the nearest populations of *G. lutescens major* in northeastern Oklahoma. Our analyses indicated that seven females from the St. Louis area population were not significantly distinguishable from *G. b. bursarius* in Kansas, and we can see no reason to recognize this population as subspecifically distinct (see further discussion below). One adult male from St. Louis County, two from Carter County, and one from Wayne County were available for study. These were entered as unknowns in the discriminant function analysis of males. The results indicate that the St. Louis specimen may be assigned to *G. bursarius* (posterior probability = 1.00), whereas those from Carter and Wayne counties are most likely *G. lutescens* (probability = 1.00, 1.00, and .898, respectively), and are closest to *G. l. major*. In the analysis of Oklahoma gophers (discussed below), these males were all assigned to *G. l. major*, with probabilities of .99, .741, and .581, rather than to *G. breviceps* from Oklahoma or *G. bursarius* from St. Louis. On this basis we have assigned the Carter and Wayne County specimens to *G. lutescens*, and have tentatively listed them as *G. l. major*. If this population is extinct, as suggested by McLaughlin, it may not be possible to assign these gophers to any taxon with any greater degree of assurance.

Nebraska region.—Pocket gophers from Nebraska, South Dakota, and Wyoming show considerable variation in body size and pelage coloration, and this has led to the suggestion that various populations should be considered subspecifically distinct (Blossom, 1938; Swenk, 1939, 1940). Each nominal subspecies was considered to be quantitatively distinct from the "typical" form of the Sandhills region in north-central Nebraska, and was thought to be confined to a certain soil and vegetation type. To test for patterns in variation of these pocket gophers, we entered all OTUs having five or more specimens (Table 1) as knowns in a discriminant function analysis. The results (Fig. 6) showed two groups; one of these, referable to *G. bursarius*, was composed of individuals found in eastern Nebraska, among which no subgroups could be distinguished on the basis of F-statistics and jackknife classification matrices. Specimens from a hybrid zone in central Nebraska (described in detail by Heaney, 1979) are discussed below. The absence of overlap between the two groups is taken as evidence of a lack of significant introgression into either species.

We found no distinct groups of OTUs within *G. lutescens* in the Nebraska region. There is a general trend for decreasing size from north to south and west to east (Table 1, Fig. 3), and although OTUs from opposite ends of this region are distinguishable, none is distinguishable from its neighbors, and all variation seems to be in the form of gradual clines.

Although we did not quantify coloration, some qualitative assessments and judgments are possible. As noted by Jones (1964), pocket gophers from north of the Niobrara River in Boyd and Keya Paha counties are darker (especially in having a large, dark mid-dorsal stripe) than those from the Sandhills region; they are not paler, as was stated by Swenk (1940). Those from immediately south of the Niobrara River in Brown and western Rock counties are dark also, as are those from south of Chadron in Dawes County, Nebraska (Swenk, 1940). In both regions the color change is rapid, defined by the Niobrara River in Boyd and Holt counties, and by Bone Creek in Brown County. The color change is correlated with change in habitat from mixed grass prairie on sandy loam soil to sandhills prairie on sandy soil in Boyd, Brown, Holt, and Keya Paha counties, and from mixed ponderosa forest-short-grass prairie on dark sandy loam to short-

grass prairie on sandy soil in Dawes County (Kaul, 1975; Swenk, 1940). A correlation between coat color and soil color has been previously documented in *Geomys* (Hendrickson, 1972), and we feel that this variation, and other, less dramatic color variation in the species elsewhere, is probably the result of local adaptation and carries little or no information about gene flow. Because we did not find concordant differentiation in cranial morphology, and in fact have evidence of broad clines in morphology, we have chosen to follow Jones (1964) in recognizing a single subspecies of pocket gopher *(lutescens)* in the western portion of Nebraska and adjacent areas.

Jones (1964) suggested that a broad zone of intergradation between *bursarius* and *lutescens* exists in Adams, Antelope, Boyd, Buffalo, Harlan, Holt, Kearney, and Webster counties on the basis of east-west clines in color and size; cranial morphology was not considered. He believed that the zone of intergradation widened towards the south, especially south of the Platte River. Lack of intergradation in Kansas, as was demonstrated above, puts his observation in doubt, and Fig. 3 shows that the size cline is discontinuous. We tested for intergradation in Nebraska by running a second discriminant function analysis in which all specimens from the above-named counties, plus those from Franklin and Wheeler counties, were entered as unknowns for comparison with a group of *G. bursarius* and of *G. lutescens*, each composed of all specimens of the respective taxa from outside the putative zone of intergradation. All specimens from Boyd, Buffalo, Custer, Dawson, Franklin, Harlan, Kearney, Kaya Paha, Valley, Webster, and Wheeler counties, and those from western Antelope County, were identified as *G. lutescens* with posterior probabilities in excess of .99. Those from Adams (1),

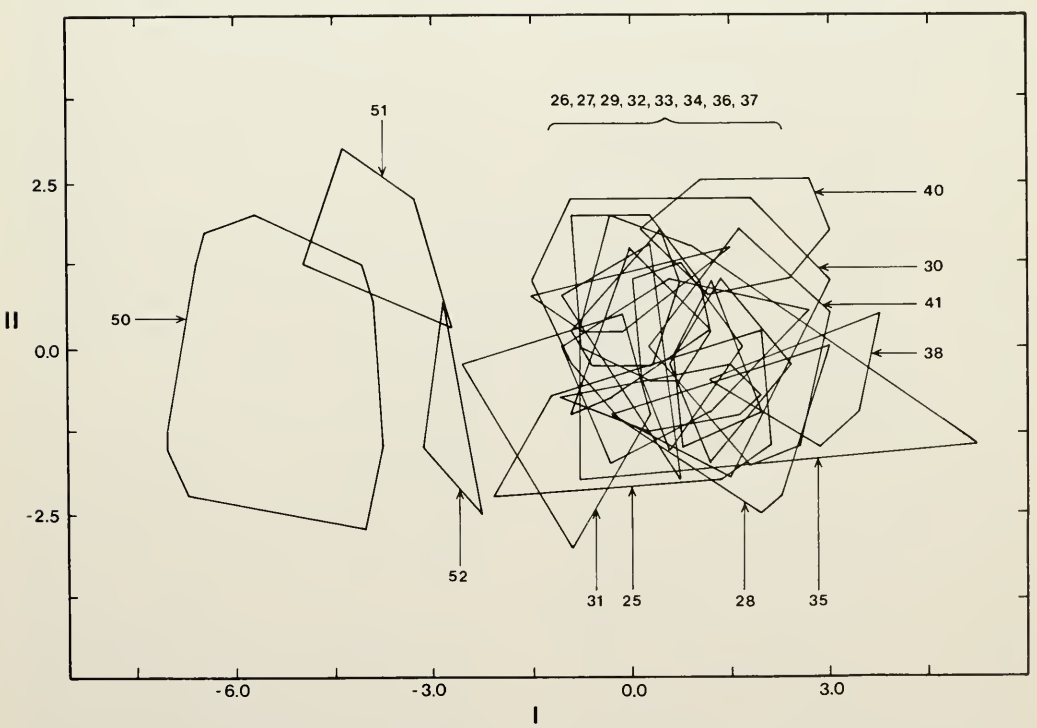

Fig. 6.—Graph of the first two axes of the discriminant function analysis of the Nebraska region OTUs. Polygons on the left are *G. bursarius bursarius*, and on the right are *G. lutescens lutescens*. Numbers correspond to OTU numbers; see text.

Knox (3), and Platte (1) counties were identified as *G. bursarius* with posterior probabilities of 1.00, .74, .99, .98, and .63. None of these specimens had qualitative features which characterized the hybrids in Antelope County (Heaney, 1979). Males from the contact area were analyzed similarly, and all specimens (Boyd, Franklin, Greeley, Harlan, Holt, Kearney, Keya Paha, and Valley counties) except one were assigned to *G. lutescens* with posterior probabilities in excess of .95. One specimen from Boyd County was assigned to *G. lutescens* with a probability of .51, but another from one mile away was assigned to *G. lutescens* with a probability of 1.00; the one "intermediate" specimen was a large, old male with qualitative features characteristic of *G. lutescens*. Also included in the analysis were males from the hybrid zone described by Heaney (1979). Specimens previously identified as *G. lutescens* were assigned to *G. lutescens* with probabilities over .95; five specimens previously identified as *G. bursarius* were identified as *G. bursarius* with probabilities of .59, .89, .95, .99, and 1.00. One specimen from Antelope County identified by Heaney (1979) as a hybrid was assigned to *G. bursarius* with a posterior probability of .81 (see also below).

We conclude that in Nebraska introgression between the two species of *Geomys* is so low that it cannot be measured by the morphometric techniques employed here, or is absent altogether. However, there are few specimens from many parts of the potential zone of contact, and further studies are warranted.

Northeastern region.—In the third series of discriminant function analyses, all OTUs from Illinois, Indiana, Iowa, Minnesota, North Dakota, eastern South Dakota, and Wisconsin were entered as knowns, and those from Kansas, Missouri, and Nebraska previously identified as *G. bursarius* were entered as knowns also. The results (Fig. 7) indicated that the Indiana and Illinois samples, although not distinguishable from each other, were distinct from all other groups. These gophers were named as a subspecies of *G. bursarius (G. b. illinoensis)* by Komarek and Spencer (1931). Because they are isolated from parapatric populations by the Mississippi River (Fig. 1), there is little to no opportunity for gene flow; only one *G. b. illinoensis* was misclassified as belonging in the St. Louis area OTU, and the converse is true, also. *G. b. illinoensis* was also found to be distinct from Wisconsin pocket gophers, which also occur east of the Mississippi River; the two are separated by 300 km and several large rivers, and show no evidence of close relationship.

The Wisconsin OTU, referable to *G. b. wisconsinensis* Jackson, 1957, was nearly as distinct as *G. b. illinoensis*. The F-matrix indicated significant differences from all other OTUs, and one of the eleven specimens was misclassified as belonging with the northwestern Missouri OTU. This level of morphological distinctness contrasts with the absence of apparent karyological differences (discussed below). Females from Chippewa (1) and Polk (2) counties were entered as unknowns in a discriminant function analysis in which all *G. b. bursarius, G. b. illinoensis,* and *G. b. wisconsinensis* were grouped as three units. The specimens from Polk County were assigned to *G. b. bursarius* with a probability of .81 and .99, and the one from Chippewa County was assigned to *G. b. wisconsinensis* with a probability of .54. Two males from Trempealeau County were both assigned to *G. b. bursarius* with a probability of .98. The intermediate position of the specimen from Chippewa County may indicate some introgression. Nevertheless, we retain *G. b. wisconsinensis* as a valid subspecies because the qualitative and quantitative differences suggest that some selective forces have acted on it separately from other members of the species, perhaps during a period of allopatry during the late Pleistocene (see below). Studies in northwestern Wisconsin, where *G. b.*

bursarius and *G. b. wisconsinensis* meet, may clarify the relationship between the two.

All other OTUs included in this analysis overlapped with each other extensively, and variation appears to be clinal (Fig. 7); for example, OTUs from Minnesota and Kansas are distinguishable, but they both overlap with OTUs from Iowa and eastern Nebraska. Division of this large population into subspecies would be arbitrary and would not impart any information about relationships, so we have chosen to recognize all OTUs as belonging to a single subspecies, *G. b. bursarius*. This is contrary to Swenk (1940), Villa-R. and Hall (1947), Bowles (1975), and Hall (1981) who divided the gophers into two subspecies, *G. b. bursarius* and *G. b. majusculus*. We also include *G. b. missouriensis* in *G. b. bursarius*. As discussed above, as originally defined, this subspecies was composed of populations of two species. The northern populations near St. Louis are not distinguishable from pocket gophers from eastern Kansas. Because the holotype is from St. Louis, *G. b. missouriensis* should be regarded as a junior synonym of *G. b. bursarius*. The southern populations, from Wayne and Carter counties, are here referred to *G. l. major*, as discussed above.

Oklahoma region. — Discriminant function analysis of gophers from Oklahoma, Arkansas, and Missouri indicated the presence of three principal groups (Fig. 8). Gophers from eastern Oklahoma (OTUs 79 and 80) are clearly distinct from those elsewhere in the region, and the specimens from adjacent counties (OTU 78) were indistinguishable from these. These specimens are referable to *G. breviceps sagittalis* (Honeycutt and Schmidly, 1979). Gophers from central and western Okla-

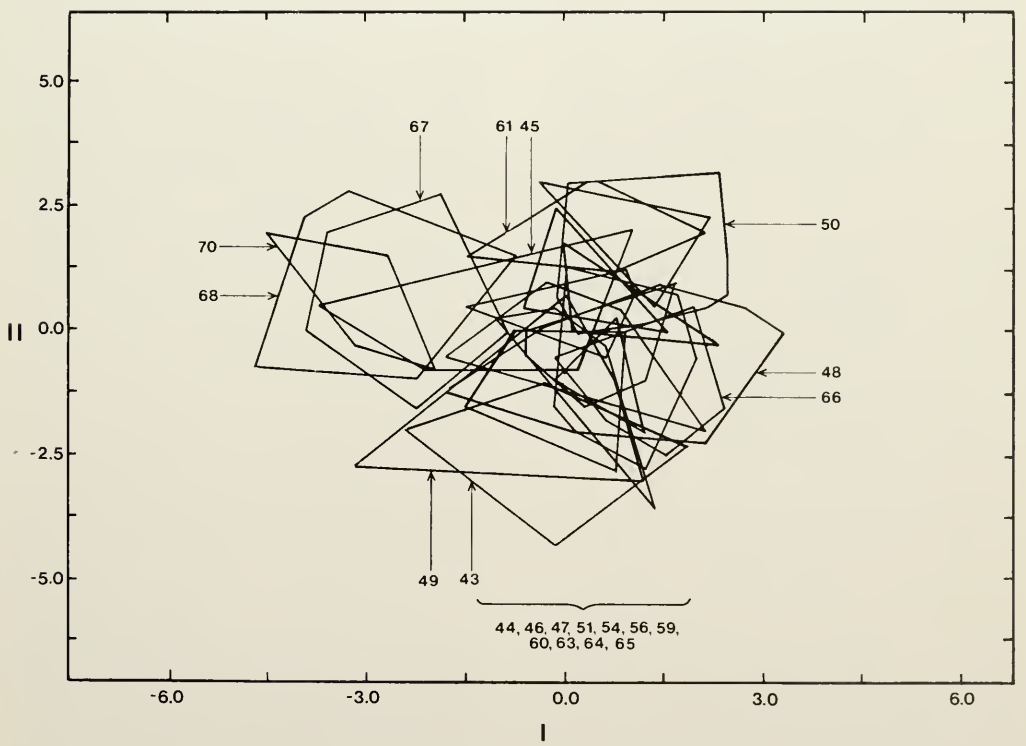

FIG. 7.—Graph of the first two axes of the discriminant function analysis of the Northeastern region OTUs. Polygons 67, 68, and 70 represent *G. b. illinoensis;* 66 represents *G. b. wisconsinensis;* and all others are *G. b. bursarius*. Numbers correspond to OTU numbers; see text.

homa formed a second cluster of widely overlapping groups (OTUs 72, 73, 75, and 76); these are referable to *G. lutescens major*. A final cluster is formed by gophers from northern and eastern Missouri (OTUs 49, 53, and 54). Although this last cluster falls close to *G. l. major* on the graph, no specimens from either group were misidentified as belonging to the other.

Baker and Glass (1951) studied a series of 31 *Geomys* from Pottawatomie and Cleveland counties, Oklahoma, and concluded that the two characters used previously to distinguish between *major* and "*dutcheri*" (= *sagittalis*) (namely, length of hind foot and relative length of dorso-lateral exposure of the jugal) showed evidence that the two taxa intergraded. They also noted a line of contact between the taxa running from Pawnee through Lincoln, Cleveland, Pottawatomie, and McClain counties. To test their hypothesis of widespread intergradation, we conducted a discriminant function analysis in which gophers from the OTUs mentioned above were entered as three groups of knowns, and all specimens from the following counties in central Oklahoma were entered as unknowns: Canadian, Cotton, Creek, Garvin, Grady, Jefferson, Kay, Lincoln, Love, McClain, Okfuskee, Oklahoma, Payne, Pottawatomie, Stephens, and Tulsa. We found evidence for "intergradation" or close contact only in Cleveland, Grady, McClain, Oklahoma, Payne, and Pottawatomie counties. In Canadian, Cotton, Jefferson, Kay, and Stephens counties, all gophers were assigned to *G. l. major* with probabilities in excess of .90, and in Creek, Garvin, Love, Okfuskee, and Tulsa counties all were assigned to *G. breviceps* with probabilities in excess of .85. The two specimens from Lincoln County were identi-

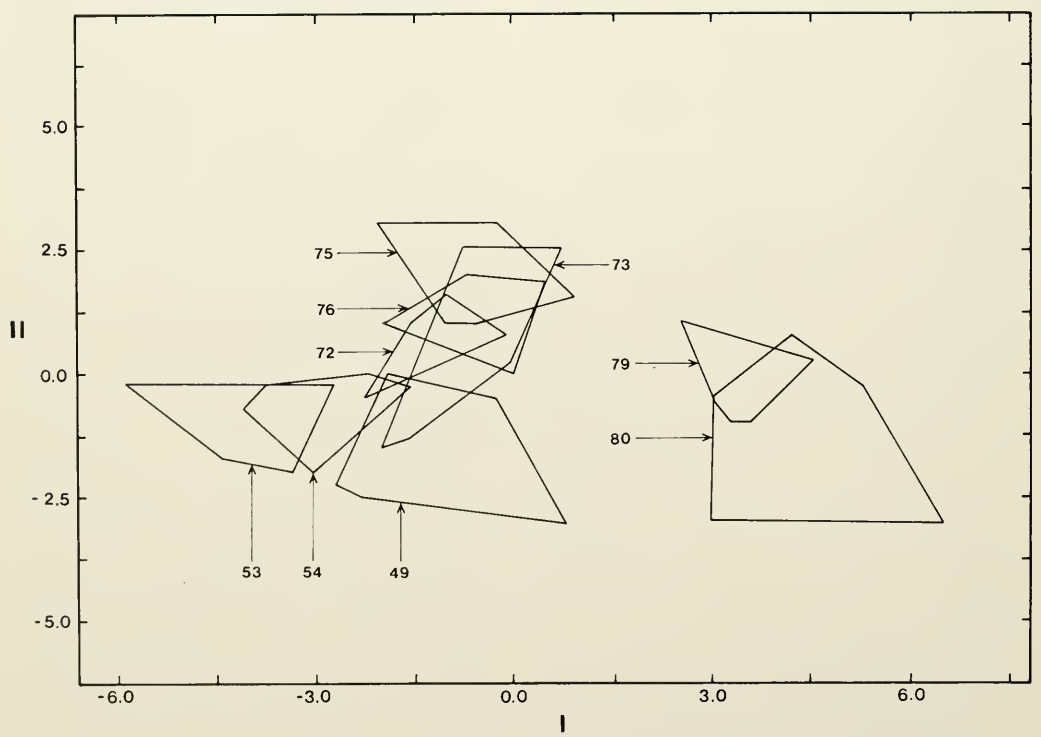

Fig. 8.—Graph of the first two axes of the discriminant function analysis of the Oklahoma region OTUs. Polygons on the right are *G. breviceps sagittalis*, those in the upper left are *G. lutescens*, and those in the lower left are *G. bursarius*. Numbers correspond to OTU numbers; see text.

fied as *G. l. major*, but both are large, old adults (one male and one female) and have qualitative features typical of *G. breviceps*. We tentatively refer these to *G. breviceps*, but recognize the need for additional information.

Our analysis included all adults from Cleveland and Pottawatomie counties used by Baker and Glass (1951). Unfortunately, many they included were not full adults, and so could not be utilized here, but some additional specimens were available to us. We found that, contrary to statements by Baker and Glass (op. cit.), three adult specimens from Pottawatomie County are clearly identifiable as *G. lutescens* (female from 1 mi. S Tecumseh, prob. = 1.00) or *G. breviceps* (two males from Asher, prob. = .98, .99). These are from two distinctly different soil and vegetational types. The *G. lutescens* are from an extensive area of oak-hickory savannah on light-colored sandy soil, whereas *G. breviceps* are from riverine forest and saturated floodplain along the Canadian River. In Cleveland County, our examination of 24 females and 15 males from the vicinity of Norman revealed that there is an abrupt contact between *G. lutescens* and *G. breviceps*. Specimens assigned to *G. breviceps* and *G. lutescens* meet in an apparent zone of intergradation extending from central Norman to about three miles east of Norman; possible hybrids are from 1½ mi. E Norman (SM 10835), 2.85 mi. E Norman (SM 10842), and ½ mi. S Norman (USNM 263479). Unfortunately, we have too few specimens to document the north-south extent of the zone. Hart (1978) found gophers with karyotypes typical of *G. breviceps* at 4 mi. E Norman, and typical *G. l. major* in Norman, further identifying this as a contact zone. The vicinity of Norman was originally tall-grass prairie on dark, clayey soils, with an oak-hickory savannah on sandy soil a few miles to the west (Gray, 1959), but agriculture and urbanization have undoubtedly had a major impact. At present, we feel that such a narrow zone indicates either a recent contact between the taxa, which seems unlikely, or past selection against introgression. Detailed studies currently underway by Zimmerman (pers. comm.) should clarify the dynamics and significance of the hybrid zone.

From Payne County, to the north of Cleveland County, we examined nine adult females and six adult males, all from near Stillwater. There appears to be an abrupt contact between *G. lutescens* and *G. breviceps* just to the west of Stillwater, with possible hybrids from 4 mi. N (OSU 497) and 2 mi. S (OSU 8407) of Stillwater. Another apparent hybrid (prob. of belonging to *G. breviceps* of 58%) is from 1 mi. W Perkins Corner (OSU 2594), which is 10 miles south of Stillwater. All of those west of Stillwater are typical *G. lutescens*, and those to the east are *G. breviceps*, but our sample sizes are too small to allow definitive conclusions. Like Norman, Stillwater originally was tall-grass prairie on dark, clayey soil, but it has been greatly disturbed by human activity. Also like Norman, a pocket of light sandy soil that once supported oak-hickory savannah occurred nearby (to the south and west).

A third contact area between *G. breviceps* and *G. l. major* exists in Oklahoma County. Two specimens from 2 mi. E Tinker Field (adjacent to Oklahoma City) both have .99 probability of belonging to *G. breviceps*, whereas three from Oklahoma City were assigned to *G. l. major* (prob. = .99, .99, and .92). No specimens from intervening areas are available.

In McClain County, two specimens from 2 mi. W Byars and Rosedale were assigned to *G. breviceps* (prob. = .94 and 1.00, respectively), whereas a specimen from about 10 miles to the west at Wayne was assigned to *G. l. major* (prob. = .99); all were in dark, clayey soils under tall-grass prairie, but several other soil types occur very close by. Finally, in Grady County, a specimen from riverine floodplain at 1 mi. W

Chickasha was assigned to *G. breviceps* (prob. = .98), whereas a specimen from about 15 miles away in a sandy soil/oak-hickory savannah association (Gray, 1959) at ½ mi. S, 3 mi. W Blanchard was assigned to *G. l. major* (prob. = 1.00).

The above soil and vegetation designations were taken from a map prepared by Gray (1959). When the various localities from which *Geomys* have been taken in Oklahoma are plotted, it is apparent that *G. l. major* is associated with light-colored, moderately sandy, well-drained soils underlying short-, mid-, or tall-grass prairie. *G. breviceps sagittalis*, on the other hand, is associated with dark-colored clayey or moist riverine soils under oak-hickory savannah or tall grass. *G. breviceps* apparently is entirely absent from the Ozark and Ouachita Highlands where oak-hickory-pine savannah and forest predominate. The two taxa do show some ability to move into "atypical" habitat away from the general area of contact. In the Payne to Grady counties contact zone, interdigitation of soil and vegetation types creates an extremely complex pattern. In spite of this, affinity of the two taxa to their usual soil type is moderately strong, with *G. l. major* nearly always found in or near extensive sandy soils and *G. breviceps* in or near darker soil that supports some trees, as well as tall-grass prairie. The zone of contact meanders due to interdigitation of soils, but where specimens are available, the potential zone of introgression appears to be no more than five miles wide, and may be much less. These data all indicate to us that *G. breviceps* and *G. l. major* are ecologically and evolutionarily independent of one another, and should be recognized as distinct species. Studies of chromosomal variation support this hypothesis (Honeycutt and Schmidly, 1979; Tucker

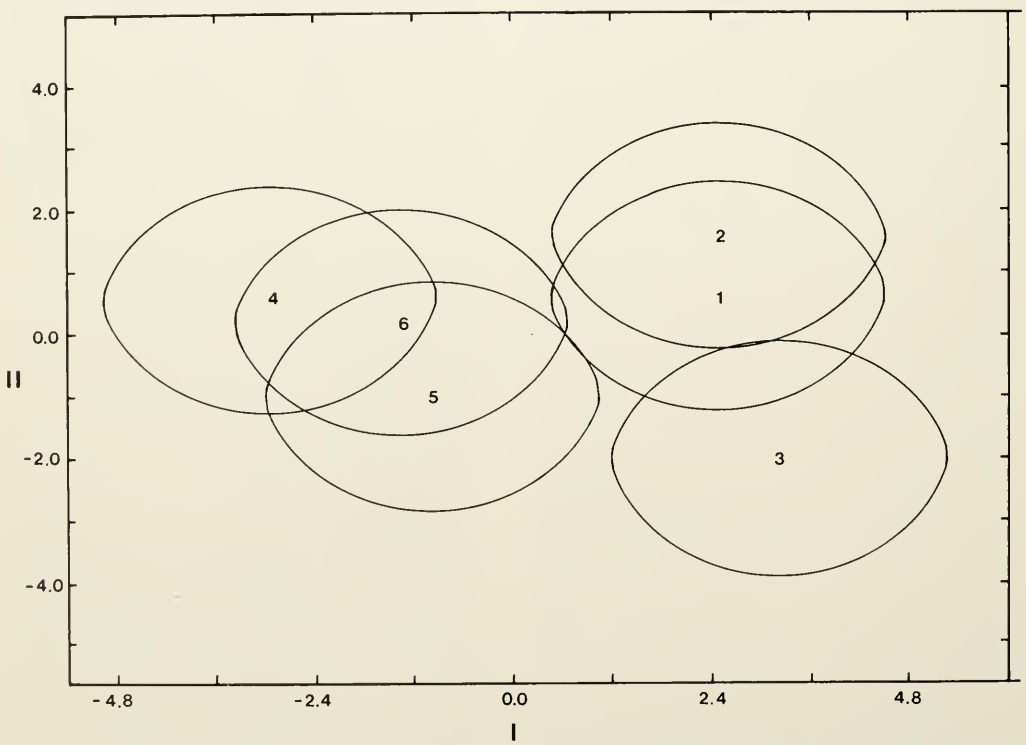

Fig. 9.—Graph of the first two axes of the discriminant function analysis of all taxa. I = *Geomys bursarius bursarius*, 2 = *G. bursarius wisconsinensis*, 3 = *G. bursarius illinoensis*, 4 = *G. breviceps sagittalis*, 5 = *G. lutescens lutescens*, 6 = *G. lutescens major*. Elipses enclose approximate 95% confidence limits. For classification functions, see Table 4.

and Schmidly, 1981), and current testing by Zimmerman (pers. comm.) should clarify the matter still further.

As mentioned above, gophers from Arkansas were also included in this analysis. We have only three adult females and nine males available from a total of four counties, however, so our results must be considered to be tentative.

One male and one female from Crawford County, which is adjacent to Oklahoma, were assigned to *G. breviceps* with probabilities of 1.00 for both. Two males from Saline County, in central Arkansas, also were assigned to *G. breviceps* (prob. = 1.00, .83). However, in Pulaski County, which is immediately to the east of Saline County, one male was assigned to *G. breviceps* (prob. = .78), four males (prob. = .83, .99, .95, .99) were assigned to *G. l. major,* and one female and one male were essentially intermediate (prob. of belonging with *G. breviceps* = .55 and .47, respectively). Our one specimen from Ouachita County was a young male, but seemed typical of *G. breviceps.* We consider it possible that the population of *G. l. major* from southern Missouri once extended to Pulaski County, but we feel that much more evidence is needed before this can be stated with confidence. For now, we list all Arkansas gophers as *G. breviceps sagittalis* as a matter of convenience, but emphasize that this is a tentative assignment in need of further investigation.

As indicated in the Kansas region analysis, gophers from Missouri fall into two species. All gophers from northern Missouri and the St. Louis area appear to be typical *G. b. bursarius,* and three specimens from south of St. Louis in Crawford, Franklin, and Perry counties were assigned to *G. bursarius* (prob. all in excess of .95). The populations from Carter and Wayne counties were assigned to *G. l. major,* as discussed above. In this case there is little evidence against assigning them to *G. l. major,* and we have done so, but further studies are warranted.

Discriminant functions analysis of

TABLE 3.—Means (± standard deviation) of measurements from adult female *Geomys.* Specimens from areas of contact between taxa (see text) are not included.

	G. bursarius bursarius	*G. bursarius wisconsinensis*	*G. bursarius illinoensis*	*G. breviceps sagittalis*	*G. lutescens lutescens*	*G. lutescens major*
N	181	11	42	23	321	133
Total Length	266.2 ±17.0	269.3 ±13.4	269.0 ±15.2	214.9 ± 9.4	239.8 ±12.6	238.9 ±13.8
Tail Length	74.5 ± 7.9	81.3 ± 6.5	81.4 ± 7.4	66.5 ± 7.5	70.0 ± 7.6	71.5 ± 7.2
Hind Foot	33.6 ± 2.0	33.3 ± 1.3	32.4 ± 1.9	26.7 ± 2.0	30.6 ± 1.76	30.4 ± 1.8
Condylobasal Length	47.42 ± 2.03	47.11 ± 1.53	48.36 ± 1.16	39.57 ± 1.30	42.04 ± 1.38	42.07 ± 1.35
Zygomatic Breadth	28.77 ± 1.39	28.32 ± 0.79	28.83 ± 1.64	24.77 ± 0.87	26.32 ± 1.09	26.20 ± 1.11
Mastoid Breadth	26.70 ± 1.42	25.84 ± 0.79	27.43 ± 0.86	22.74 ± 0.62	24.06 ± 0.91	24.66 ± 0.94
Nasal Breadth	9.81 ± 0.45	9.51 ± 0.19	9.93 ± 0.28	8.67 ± 0.37	9.58 ± 0.54	9.16 ± 0.35
Frontal Square Length	3.90 ± 0.63	3.13 ± 0.29	5.49 ± 0.57	2.65 ± 0.67	3.50 ± 0.57	3.89 ± 0.60
Frontal Square Breadth	1.96 ± 0.37	2.78 ± 0.34	2.01 ± 0.34	1.34 ± 0.36	1.73 ± 0.40	1.59 ± 0.34
Orbital Length	15.88 ± 0.79	15.34 ± 0.60	16.07 ± 0.42	13.62 ± 0.62	14.28 ± 0.60	14.58 ± 0.59
Maxillary Visibility	0.76 ± 0.42	0.59 ± 0.49	0.84 ± 0.34	0.26 ± 0.42	0.40 ± 0.48	0.81 ± 0.39

taxa.—A final discriminant function analysis was run on all members of the six taxa; this included 711 specimens (means in Table 3), and excluded those from contact areas (92 specimens). Scatter along the first two axes is shown in Fig. 9, and classification functions for the first axis are given in Table 4. The jackknifed classification matrix indicated that only 11 out of 454 (2.4%) *G. lutescens* were misclassified as *G. bursarius*, and 13 (2.9%) were misclassified as *G. breviceps*. Of 234 *G. bursarius*, 16 (6.8%) were misclassified as *G. lutescens*, and none as *G. breviceps*. However, 10.7% and 19.6% of the *G. bursarius* and *G. lutescens*, respectively, were misclassified as to subspecies within the proper species. These data reflect the higher level of morphological distinctness between than within species.

CLUSTER ANALYSIS OF THE TAXA

A final quantitative analysis of morphological similarity was conducted using a cluster analysis of all taxa (Fig. 10), based on the results of a principal components analysis (see Methods). The analysis indicates that two major groups are present. The first group consists of the three subspecies of *G. bursarius*, with *G. b. wisconsinensis* being the most distinct of the three. The second group contains both *G. breviceps* and *G. lutescens*. The analysis indicates a roughly equivalent level of distinctness in the pairs *G. l. lutescens–G. l. major* and *G. b. bursarius–G. b. illinoensis*.

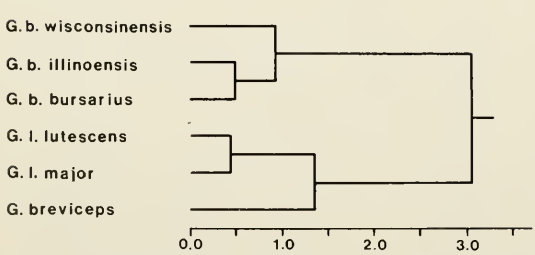

Fig. 10.—Phenogram of cranial similarity of six taxa of *Geomys* from the study area based on cluster analysis of transformed taxon means. Units on the axis are amalgamation distances.

Table 4.—Pairwise classification functions for all adult females of taxa that are parapatric. Variable names are: 1= total length; 2= tail length; 3= hind foot length; 4= condylobasal length; 5= zygomatic breadth; 6= mastoid breadth; 7= nasal breadth; 8= frontal square length; 9= frontal square width; 10= orbital length; 11= maxillary visibility.

1. *G. b. bursarius* vs. *G. b. wisconsinensis*
$$X = -0.096(V_1) + 0.535(V_2) + 0.209(V_3) - 0.827(V_4) - 0.675(V_5) + 1.686(V_6) + 3.324(V_7) + 1.448(V_8) - 6.507(V_9) + 1.523(V_{10}) + 0.223(V_{11}) - 21.995.$$
2. *G. b. bursarius* vs. *G. b. illinoensis*
$$X = 0.380(V_1) - 0.184(V_2) + 0.639(V_3) + 0.032(V_4) - 0.861(V_5) + 0.315(V_6) - 0.151(V_7) - 4.583(V_8) - 1.729(V_9) + 0.299(V_{10}) - 0.758(V_{11}) + 20.427.$$
3. *G. b. bursarius* vs. *G. l. lutescens*
$$X = 0.0156(V_1) - 0.094(V_2) + 0.232(V_3) + 2.968(V_4) - 0.736(V_5) + 0.223(V_6) - 3.859(V_7) + 0.059(V_8) + 0.350(V_9) + 0.493(V_{10}) + 0.107(V_{11}) - 93.689.$$
4. *G. b. bursarius* vs. *G. l. major*
$$X = 0.039(V_1) - 0.156(V_2) + 0.316(V_3) + 3.361(V_4) - 0.123(V_5) - 1.440(V_6) - 1.780(V_7) - 0.663(V_8) + 0.549(V_9) - 0.446(V_{10}) - 1.087(V_{11}) - 92.250.$$
5. *G. l. major* vs. *G. l. lutescens*
$$X = -0.024(V_1) + 0.065(V_2) - 0.084(V_3) - 0.393(V_4) - 0.613(V_5) + 1.663(V_6) - 2.079(V_7) + 0.722(V_8) - 0.199(V_9) + 0.939(V_{10}) + 1.939(V_{11}) - 1.439.$$
6. *G. breviceps sagittalis* vs. *G. l. major*
$$X = -0.071(V_1) + 0.047(V_2) - 0.790(V_3) + 0.752(V_4) + 0.565(V_5) - 0.946(V_6) - 1.811(V_7) - 3.350(V_8) - 1.995(V_9) - 1.233(V_{10}) - 2.784(V_{11}) + 61.932.$$
7. *G. breviceps sagittalis* vs. *G. l. lutescens*
$$X = -0.095(V_1) + 0.112(V_2) - 0.358(V_3) + 0.359(V_4) + 0.134(V_5) + 0.716(V_6) - 3.890(V_7) - 2.628(V_8) - 2.195(V_9) - 0.293(V_{10}) - 1.590(V_{11}) + 60.493.$$

CRANIAL MORPHOLOGY OF GOPHERS IN THE ANTELOPE COUNTY, NEBRASKA CONTACT ZONE

As noted in the discussion of gophers from Nebraska, specimens that appear to be hybrids between *G. bursarius* and *G. lutescens* are available from a single, very limited area near Oakdale, Antelope County. The town of Oakdale lies about 1.5 km east of the extreme eastern edge of the Nebraska Sandhills. To the east

of Oakdale, tall-grass prairie predominates, and the soil is generally silty loam; to the west of Oakdale is short-grass prairie that lies on the sandy soil of the Sandhills. Results described above show that two readily distinguishable gophers, *G. bursarius* and *G. lutescens,* occur in the tall-grass/silty loam association and short-grass/sandy soil association, respectively, and no intergradation could be detected on a broad scale. We examined 30 adult females and 14 adult males from the vicinity of Oakdale (Table 5; Appendix 1), with a special interest in those from 0.5 to 1.5 km west of Oakdale, where the two soil and vegetation types come into contact and intergrade. Details of soil and plant distributions, and gopher distribution and reproduction are provided by Heaney (1979). We provide data here on cranial morphology that is critical to determining the presence of hybridization and the width of the hybrid zone.

In order to quantify the rapidity of change in cranial morphology of gophers in the contact area, a series of stepwise discriminant function analyses (BMDP7M) was conducted. A reference sample of *G. bursarius* from Butler, Gage, Knox, Lancaster, Madison, and Platte counties, Nebraska, and a sample of *G. lutescens* from western Antelope, Custer, Dawson, Greeley, and Valley counties, Nebraska, were used as typical representatives of those taxa; males and females were analyzed separately, and only adults were used. These samples were chosen because they are geographically adjacent to the contact zone, so that the direct and indirect effects of climate on variation should be minimal. In these analyses, all specimens from the study area were entered as "unknowns" to be compared with the two reference samples.

In the analysis of females, a combination of three variables, considered simultaneously, was found to be the best method of distinguishing between reference samples of *G. bursarius* and *G. lutescens;* these were condylobasal length, hind foot length, and frontal square length. An F-to-enter of 4.0 was used as a stopping criterion for determining the number of variables to be included. All specimens of the two reference samples were correctly identified to species by the classification function that was generated, and the two samples were significantly different ($p < 0.01$). Females from the study area were plotted in Fig. 11 using the same classification function; thus, their positions along the discriminant axis indicate their relative similarity to *G. bursarius* or *G. lutescens.* There is a significant correlation between discriminant scores and distance west of Oakdale ($r = 0.733$; $p < 0.01$). Reference samples of *G. bursarius* and *G. lutescens* were not included in this regression.

Males from this area (Fig. 12) were subjected to the same type of analysis, again using an F-to-remove of 4.0 as stopping criterion. The variables which entered as significant were total length, zygomatic breadth, mastoid breadth, and appearance of the posterior portion of the maxillary. The classification matrix indicated that reference samples were significantly different from one another ($p < 0.05$), but also that one member of each reference sample (i.e., 6%) was mistakenly identified by this classification function as belonging to the wrong species. As with the females, the correlation between discriminant score and distance west of Oakdale is significant ($r = 0.654$, $p < 0.05$). For both males and females, visual inspection of the graphs indicates that most of the change occurs at about 1.5 km west of Oakdale, at the extreme eastern edge of the Sandhills. The fact that specimens of intermediate morphology exist, and that the variation is nearly continuous, suggests that introgression probably takes place. However, introgression must be slight, since the change from typical *G. bursarius* cranial morphology to typical *G. lutescens* morphology takes place over a distance of no more than two km, with most of the change occurring over a dis-

TABLE 5.—Measurements (mean ± standard deviation) of the five groups of *Geomys* from the contact zone near Oakdale, Antelope County, Nebraska, used in discriminant function analyses.

	Reference *G. bursarius*		Study Area *G. bursarius*		Reference *G. lutescens*		Study Area *G. lutescens*		Hybrid	Hybrid
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
n	25	14	8	5	18	18	8	8	14	1
Total length	275.4±11.7	314.2±19.8	274.1±10.0	312.8±17.5	234.6±25.3	267.7±16.6	238.6±11.1	276.9±10.3	249.5±7.4	281
Tail	75.1± 6.2	84.1±10.4	78.9± 4.5	91.2± 7.9	69.9± 8.3	77.5± 7.6	69.9± 8.3	84.8± 5.3	74.1±5.8	82
Hind foot	34.7± 1.6	37.9± 2.8	34.3± 1.3	36.8± 1.3	29.3± 1.9	31.9± 2.9	29.3± 1.9	33.4± 0.9	30.9±0.9	34
Condylobasal length	48.6± 1.8	55.9± 4.2	47.2± 1.1	54.2± 0.5	42.1± 0.9	47.7± 2.3	42.1± 0.9	48.8± 1.3	43.1±0.9	51.5
Zygomatic breadth	29.5± 1.3	34.4± 3.0	30.0± 1.3	35.4± 1.0	26.5± 0.6	31.1± 2.2	26.5± 0.6	31.4± 1.6	26.9±1.0	30.8
Mastoid breadth	27.6± 1.5	30.9± 2.1	27.7± 0.7	31.5± 0.7	24.2± 0.7	27.1± 1.5	24.2± 0.7	27.7± 1.1	24.8±0.7	29.0
Nasal breadth	10.2± 0.4	11.0± 0.6	9.9± 0.4	11.0± 0.3	9.6± 0.4	10.5± 0.8	9.6± 0.4	10.4± 0.5	9.6±0.4	10.4
Frontal square length	3.6± 0.4	4.5± 0.6	3.9± 0.6	4.6± 0.3	4.0± 0.5	4.5± 0.5	4.0± 0.5	4.4± 0.7	3.9±0.4	4.0
Frontal square width	2.0± 0.3	2.1± 0.4	2.1± 0.2	2.2± 0.6	1.8± 0.4	1.8± 0.5	1.8± 0.4	1.7± 0.5	1.6±0.4	2.1
Orbital length	16.0± 0.7	17.5± 1.3	16.0± 0.5	18.1± 1.2	14.8± 0.5	16.3± 0.7	14.5± 0.5	16.4± 0.8	14.9±0.3	16.3
Maxillary shape	0.9± 0.3	0.9± 0.3	0.7± 0.5	0.6± 0.5	0.4± 0.5	0.3± 0.5	0.4± 0.5	0.4± 0.5	0.6±0.5	1.0

tance of less than one km. Data on bacular and chromosomal variation given below also indicates a hybrid zone less than two km wide. Given the post-Pleistocene history of the area (summarized below, and in greater detail by Heaney, 1979), it is likely that the two species have been in contact for up to 9,000 years. Because introgression is slight, as indicated by the data given here, it appears that a "fusion model" type of hybrid zone does not exist at the locality. The most likely alternatives are the "isolation" and "hybrid superiority" models; neither of these is indicative of the two taxa of gophers belonging to a single species (see Heaney, 1979; Moore, 1977).

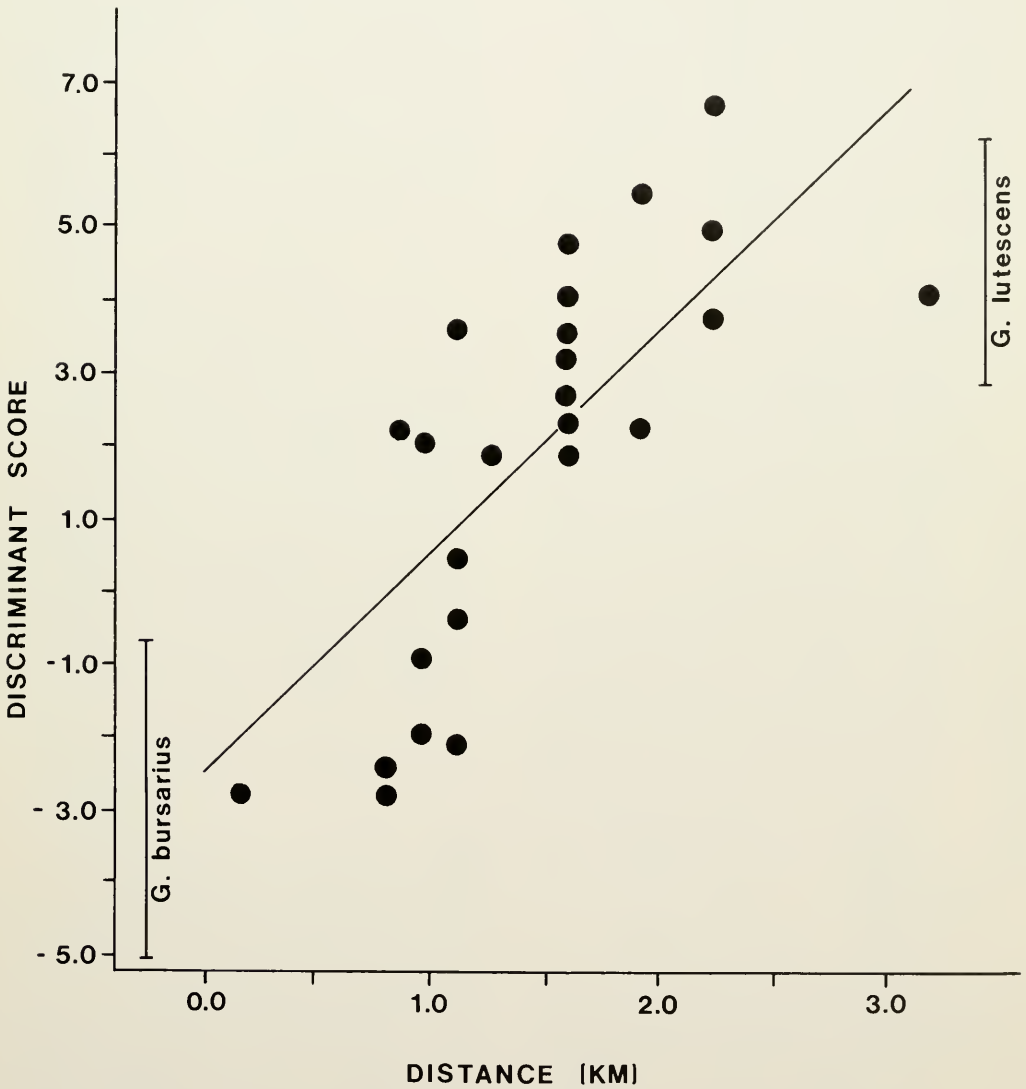

FIG. 11.—Results of discriminant function analysis of adult female *Geomys* from the vicinity of Oakdale, Antelope Co., Nebraska. Reference samples of *G. bursarius* and *G. lutescens* were entered as knowns, and all Oakdale area specimens were entered as unknowns. Ranges for the reference samples are given as vertical bars on the left and right for *G. bursarius* and *G. lutescens*, respectively. Distances given are west of the Oakdale post office. The equation for the regression line shown is: discriminant score = 5.06 (distance) −2.50. ($r = 0.733$, $p < 0.01$).

CLADISTIC ANALYSIS OF CRANIAL CHARACTERS

As noted in the descriptions of taxa given above, there are a number of cranial characters useful in distinguishing between taxa; seven of the most consistent are summarized in Tables 6 and 7. We have used these in a cladistic analysis of relationships, utilizing the Wagner Tree method (see Kluge, 1976; Carleton, 1980). We have included data on *Geomys personatus, G. pinetis,* and *Zygogeomys trichops* as well. *Geomys personatus* was considered by Merriam (1895) to be a close relative of *G. breviceps,* whereas *G. pinetis* is generally thought to be either the sister-group to all other *Geomys* (Russell, 1968), or to form a clade with *G. bursarius* and *G. lutescens,* with *G. breviceps* as the sister-group to these three (Merriam, 1895). *Zygogeomys* is thought to represent the most primitive surviving stock in the tribe to which *Geomys* belongs, the Geomyini, and is also considered the sister-group to *Geomys* (Merriam, 1895; Russell, 1968). The analysis we conducted did not include the following characters unique to *Geomys pinetis:* rostrum long and slender; incisors relatively narrow; incisors procumbent. Our objective was to evaluate relationships of the species we studied, and the re-

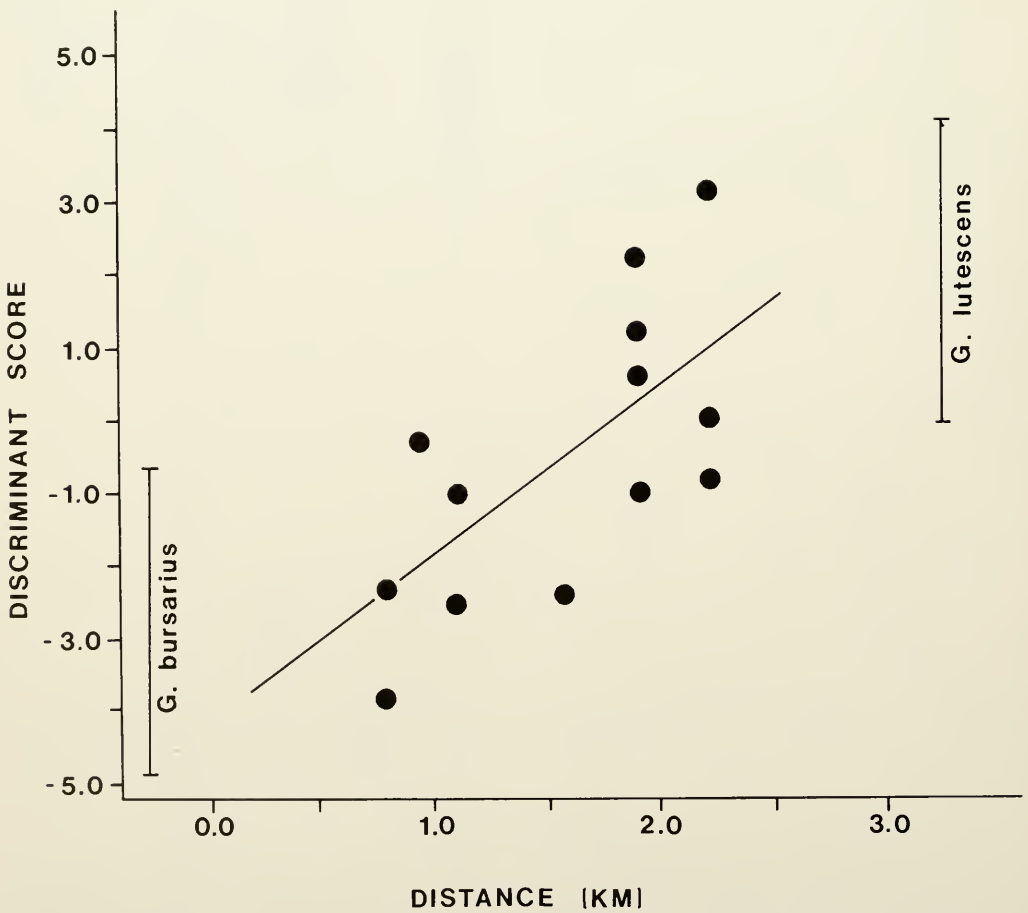

FIG. 12.—Results of discriminant function analysis of adult male *Geomys* from the vicinity of Oakdale, Antelope Co., Nebraska (see Fig. 11). The equation for the regression line is: discriminant score = 3.70 (distance) − 4.17. ($r = 0.654$, $p < 0.05$).

TABLE 6.—Summary of qualitative cranial characters that differ among taxa of *Geomys*.

OTU	Sagittal crest development (1)	Zygomatic arch width (anterior/posterior) (2)	Rostral length (3)	Mastoid process development (4)	Frontal square shape (5)	Foramen rotundum position (6)	Sublacrimal fossa (7)
1. *G. b. bursarius*	great	>1.0	long	great	long rectangle	high	deep
2. *G. b. illinoensis*	great	>1.0	very long	great	long rectangle	high	deep
3. *G. b. wisconsinensis*	great	>1.0	long	great	square	high	deep
4. *G. l. lutescens*	moderate	>1.0	short	moderate	long rectangle	high	deep
5. *G. l. major*	moderate	>1.0	short	moderate	long rectangle	high	deep
6. *G. breviceps*	slight	≈1.0	short	slight	long rectangle	low	deep
7. *G. personatus*	slight	>1.0	moderate	slight	long rectangle	high	deep
8. *G. pinetis*	slight	≈1.0	long	slight	square	high	shallow
9. *Zygogeomys trichops*	moderate	>1.0	long	moderate	short rectangle	high	shallow

sults should be viewed in that context.

Polarity of characters was based on out-group comparison with the presumed primitive sister-group, *Zygogeomys trichops*. Although this leaves open the possibility of error through character convergence of *Z. trichops* with one or more species of *Geomys*, it provides a non-arbitrary reference point that is likely to contain many primitive characters. The characters used (see Table 6) were the following.

1. Sagittal crest development.
   a. moderate
   b. slight
   c. great

In *Z. trichops*, the sagittal crest averages 2 mm wide, and varies in height from about 0.5 mm anteriorly to 1.0 mm posteriorly. *Geomys bursarius* has a higher, narrower crest, whereas the other species of *Geomys* have a broad, low ridge between the temporal crests. Because the latter group of *Geomys* vary greatly in cranial size, this does not appear to be a strictly allometric trait.

2. Zygomatic arch width.
   a. width at anterior angle greater than at posterior angle
   b. width at anterior and posterior angles approximately equal

Zygogeomys and most *Geomys* have zygomatic arches that flare laterally, then deflect posteriorly at an angle over 90°. At the level of the condylar fossa the zygoma abruptly turn and merge with the braincase. In *G. breviceps* and *G. pinetis*, the zygoma are not proportionately as broad anteriorly, so that the arches lie roughly parallel to the skull, and the width at anterior and posterior angles is approximately equal.

3. Rostral length.
   a. long
   b. moderate
   c. short
   d. very long

The rostrum and diastema of *Zygogeomys* are long, and appear to be equivalent in *Geomys b. bursarius* and *G. b. wisconsinensis;* the rostrum of *G. b. illinoensis* is even more elongate. The other species of *Geomys* have proportionately shorter rostra, with *G. pinetis* intermediate between *Zygogeomys* and the very short rostrum typified by *G. breviceps* and *G. lutescens*.

TABLE 7.—Data matrix of cranial characters coded for Wagner Tree analysis. OTUs, character numbers, and character states are from Table 6; *Zygogeomys trichops* is assumed to represent the primitive condition. Multistate characters were coded using the method described by Carleton (1980).

	G. b. bursarius	*G. b. illinoensis*	*G. b. wisconsinensis*	*G. l. lutescens*	*G. l. major*	*G. breviceps*	*G. personatus*	*G. pinetis*	*Z. trichops*
(1)	0	0	0	0	0	1	1	1	0
	1	1	1	0	0	0	0	0	0
(2)	0	0	0	0	0	1	0	1	0
(3)	0	0	0	1	1	1	1	0	0
	0	0	0	1	1	1	0	0	0
	0	1	0	0	0	0	0	0	0
(4)	1	1	1	0	0	0	0	0	0
	0	0	0	0	0	1	1	1	0
(5)	1	1	1	1	1	1	1	1	0
	1	1	0	1	1	1	1	0	0
(6)	1	1	1	1	1	0	0	0	0
(7)	1	1	1	1	1	1	1	0	0

4. Mastoid process development.
   a. moderate
   b. great
   c. slight

The mastoid process of *Zygogeomys* is prominent, robust, and triangular in dorsal view; its width (from the medial margin above the auditory canal to the margin point directly posterior) is slightly less than the length (measured lateral to the line defined by width to the lateral tip), and it is deflected at about 30° from the horizontal. In *Geomys bursarius*, the mastoid is longer than wide, and deflected at about 25°. In *G. breviceps*, *G. personatus*, and *G. pinetis*, the mastoid is of about equal length and width, and is deflected at 40° to 45°.

5. Frontal square shape.
   a. short rectangle
   b. square
   c. long rectangle

The anterior portion of the frontals lies between the posterior projections of the premaxillae, forming a small rectangle that is open on the posterior end. In *Zygogeomys* this "frontal square" is wider than it is long; in *G. pinetis* and *G. b. wisconsinensis* it is of equal length and width; and in the other species, it is longer than wide.

6. Foramen rotundum position.
   a. high on alisphenoid
   b. low on alisphenoid

The foramen rotundum of *Zygogeomys* lies high on the alisphenoid, at or near the top of the horizontal portion of the alisphenoid, and adjacent to the condylar fossa. It is usually obscured in lateral view by the zygomatic arch. The same condition is found in all *Geomys* examined except *G. breviceps*, in which the foramen rotundum lies about one-third of the way down the horizontal portion of the alisphenoid and is easily visible in lateral view.

7. Sub-lacrimal fossa.
   a. shallow
   b. deep

At the anterior edge of the orbit is a fossa that lies beneath the horizontal portion (= dorsal process) of the lacrimal. This fossa is bounded posteriorly by a thin ridge on the horizontal wall of the orbit, and ventrally by a continuation of the ridge. The fossa has a foramen that pierces its postero-ventral edge, descending ventrally into the maxillary. In *Zygogeomys* the fossa extends anteriorly only a short distance into the zygomatic root of the maxilla, the ventral foramen is small, and the ridge at the posterior margin of the fossa is low and rounded. This condition appears to be identical to that in *G. pinetis*. In all other species of *Geomys* examined, the fossa extends substantially deeper into the zygomatic

root of the maxilla, the ventral foramen is large, and the ridge at the posterior margin is high and sharp-edged.

Results of the Wagner Tree analysis are depicted in Fig. 13. *Geomys pinetis* lies closest to *Zygogeomys trichops,* i.e., possesses few derived character states that are shared with other *Geomys.* However, it should be borne in mind that the three characters related to the rostrum (cited above) that are unique to *G. pinetis* were not included in this analysis. For the characters considered, *G. pinetis* is intermediate between *Zygogeomys* and the node (#1) that links *G. breviceps* and *G. personatus.* These two species differ little from each other, and although the Wagner Tree shown illustrates *G. breviceps* as the root for *G. lutescens,* both *G. breviceps* and *G. personatus* have an equal probability of occupying this position. *Geomys lutescens* and *G. bursarius* appear to be sister-species that are derived from a *G. breviceps* or *G. personatus*-like ancestor.

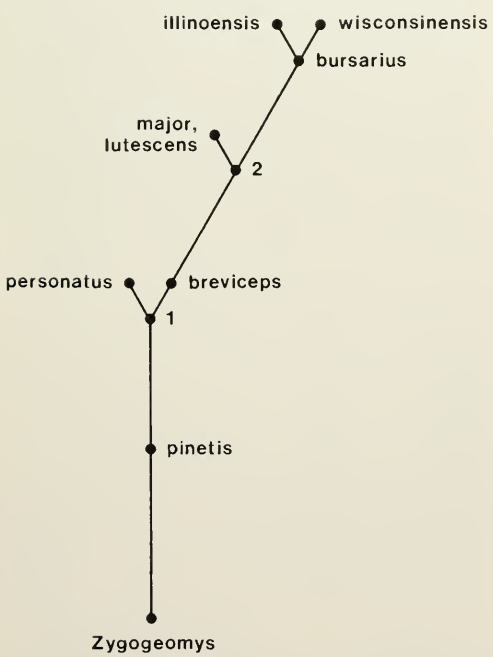

FIG. 13.—Results of a Wagner Tree analysis of seven cranial characters, using data in Table 6. Index of consistency = 0.667. Nodes 1, 2, and 3 represent hypothetical ancestors for the various clades.

The analysis suggests that the break of *G. pinetis* from the ancestral stock was an early one, and that *G. personatus* and *G. breviceps* are species that have retained traits that are similar to the population that gave rise to *G. lutescens,* and subsequently to *G. bursarius.*

ANATOMY OF THE GLANS PENIS AND BACULUM

The anatomy of the male reproductive tract has been shown to provide useful taxonomic characters in many groups of mammals (e.g., Burt, 1960; Carleton, 1980). However, the anatomy of the glans penis has not previously been described in *Geomys,* and few observations have been made on bacula of *Geomys.* Sherman (1940) illustrated a baculum of *Geomys fontanelus* (=*G. pinetis fontanelus;* see Williams and Genoways, 1980), and Burt (1960) illustrated a baculum from *Geomys bursarius bursarius.* Kennerly (1958) pointed out that some variation exists among species of *Geomys.*

We examined the glandes penes of three adult *Geomys bursarius bursarius* and three *G. lutescens lutescens,* and found no substantial variation from the morphology shown in Fig. 14, although specimens of *G. l. lutescens* were not well preserved. The glans is cylindrical and is entirely covered with evenly-spaced, extremely small tubercles. Each tubercle has two rows of spines that are directed posteriorly; each row had three to four spines (Fig. 14). The glans measures about 5 mm, with a tip (bacular mound) extending some 2.5 mm beyond. The rim of the terminal crater is slightly flared, and in lateral or dorsal view obscures the urethral pore, urethral lappets, and other features within the terminal crater. The raphe (mid-ventral ridge) is distinct but low and narrow, extending the entire length of the glans. The baculum is visible under strong light within the semi-transparent bacular mound. The mound is nearly as broad as it is long; there is no cartilaginous tip on the baculum. The structure described

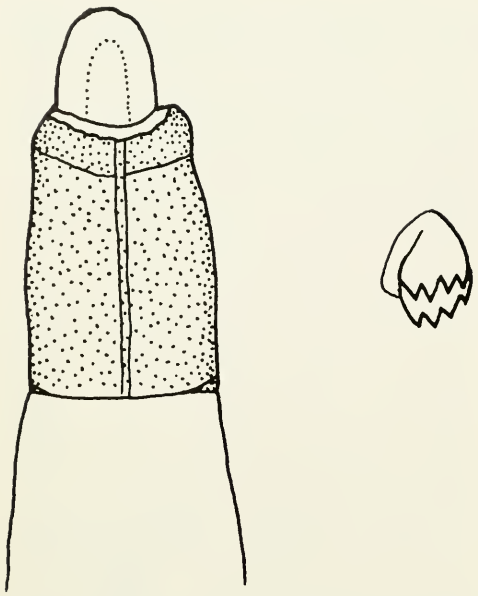

FIG. 14.—Glans penis of an adult *Geomys bursarius bursarius* from Anoka Co., Minnesota. On right is an enlargement of a tubercle from the lower right on the glans.

and illustrated here is nearly identical to that exhibited by *Liomys* and *Heteromys*, except that both heteromyid genera lack tubercles on the glans (Genoways, 1973).

Our small samples of glandes from the two species of *Geomys* failed to show differences between species, but this was not the case for the bacula we examined. As described by Burt (1960), all bacula were simple rod-like bones, with the rounded shaft curving gently upwards. The distal tip is laterally expanded and dorsoventrally flattened (Fig. 15). Table 8 lists measurements for *G. bursarius*, *G. l. lutescens*, and *G. l. major*, and gives values for a single example of *G. breviceps sagittalis*. We found that basal width varied greatly, and that it appeared to be correlated with age of the gopher. Midshaft width showed less variation, and no obvious correlation with age, once adult size (and presumably breeding condition) was reached.

The bacula of *G. bursarius* were the largest we examined on average, although those of *G. l. major* were only slightly smaller. The bacula of *G. bursarius* were generally more robust than those of *G. l. major* (Fig. 15), although this was not reflected in the midshaft diameter/length ratio (Table 8).

The bacula of *G. l. lutescens* were shorter than those of *G. bursarius* or *G. l. major*, but averaged appreciably wider at midshaft, and all gave the appearance of being more robust overall.

Our one specimen of *G. breviceps sagittalis* was much smaller than any

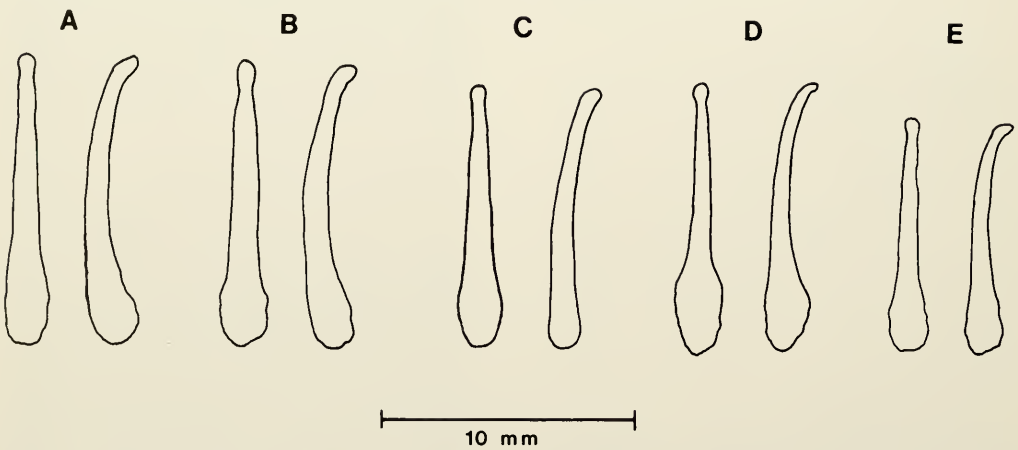

FIG. 15.—Bacula of adult *Geomys*. A = *G. bursarius bursarius* from Jasper Co., Iowa (UMMZ 81848). B = hybrid *G. b. bursarius* × *G. l. lutescens* from 1 mi. W Oakdale, Antelope Co., Nebraska (KU). C = *G. lutescens lutescens* from Brown Co., Nebraska (KU). D = *G. lutescens major* from Cimarron Co., Oklahoma (UMMZ 99612). E = *G. breviceps sagittalis* from Love Co., Oklahoma (UMMZ 99722).

TABLE 8.—Measurements and proportions (mean ± standard deviation) of bacula of *Geomys*.

Taxon	N	Length	Width of Base	Midshaft Width	Midshaft width / Length
G. b. bursarius	5	11.32±0.46	1.82±0.19	0.95±0.08	0.084 ±0.007
G. breviceps sagittalis	1	9.56	1.69	0.79	0.0826
*G. attwateri**	9	9.86	1.70	—	—
G. l. lutescens	8	10.78±0.41	1.98±0.42	1.12±0.14	0.105 ±0.014
G. l. major	4	11.21±0.11	2.09±0.33	0.94±0.15	0.083 ±0.014
G. b. bursarius × *G. l. lutescens*	1	11.68	1.94	1.21	0.104

* = from Kennerly, 1958

other. It was similar in size and appearance to nine bacula of *G. attwateri* described by Kennerly (1958), and was proportioned much the same as *G. bursarius* and *G. l. major.*

Although the morphology of the bacula generally indicates the distinctness of these four taxa, we find the degree of difference between *G. l. lutescens* and *G. l. major* to be surprising. It would be worthwhile to examine bacula from gophers from the putative zone of intergradation between the two taxa, but no specimens are currently available to us.

We also examined bacula from ten adult gophers from an area of contact and apparent hybridization between *G. b. bursarius* and *G. l. lutescens* in Antelope County, Nebraska (see Heaney, 1979, and above). Fig. 16 is a graph of the midshaft diameter/length ratio for all specimens from this contact zone, with the ranges and means for *G. b. bursarius* and *G. l. lutescens* from outside the zone for scale. Although the data are scanty, it appears that at least a few gophers from the area about one mile west of Oakdale (the eastern edge of the hybrid zone) have bacula intermediate between typical representatives of the two taxa, and that substantially more variation exists in the population in the contact zone than is usual for populations elsewhere.

In summary, the taxa of gophers examined in this study all appear to have bacula differing recognizably from each other. Most differences are in size, and appear to be correlated with the overall size of the animal. *Geomys lutescens lutescens* has the most distinctive baculum, in that it differs from the others in relative mid-shaft width. A contact zone between *G. b. bursarius* and *G. l. lutescens* yields gophers with unusually variable bacula, with no consistent indication of intermediacy.

KARYOTYPIC EVIDENCE

Few pocket gophers from the northern portion of our study area (i.e., north

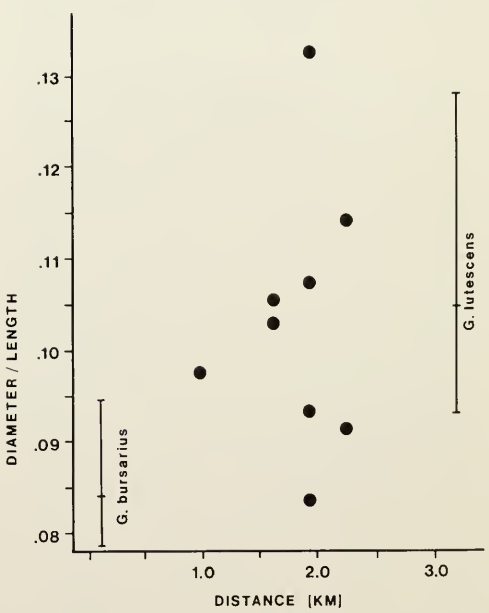

FIG. 16.—Morphology of bacula of adult *Geomys* from the vicinity of Oakdale, Antelope Co., Nebraska. Ranges for reference samples of *G. bursarius* and *G. lutescens* are from Table 8. Distances given are distance west of the Oakdale post office.

of Oklahoma) have been karyotyped; all previously available information was summarized by Hart (1978). He found that *Geomys* from Wisconsin, Iowa, and east-central Missouri had the same karyotype (2N = 72, FN = 72, 2 biarmed autosomes), and these differed only slightly from gophers from Illinois and eastern Kansas (2N = 72, FN = 70, no biarmed autosomes), and eastern Nebraska and eastern South Dakota (2N = 70, FN = 68, no biarmed autosomes). This group is what we consider to be *Geomys bursarius* sensu stricto. Thus, the karyotype for this species is 2N = 70-72, FN = 68-72, and the X chromosome is a large metacentric in southeastern South Dakota and eastern Nebraska, whereas in all other parts of the range the X is a large acrocentric.

More detailed chromosomal data are available for *Geomys* from Oklahoma, Texas, and New Mexico (Baker *et al.*, 1973; Baker and Genoways, 1975; Hart, 1978). *Geomys lutescens knoxjonesi* (2N = 70, FN = 68-70, 0-2 biarmed autosomes) has a karyotype much like that of *G. l. major* (2N = 70, FN = 70, 0-2 biarmed autosomes) (Baker and Genoways, 1975; Hart, 1978). Hart (1978) reported that the karyotype of populations previously recognized as *industrius* had autosomes identical to those of *major*, the only difference being that in the *industrius* populations, the X was a large metacentric whereas in *major* it was a large acrocentric. Other members of *G. lutescens* (= the "*lutescens* group" of Honeycutt and Schmidly, 1979) are *G. lutescens texensis* and *G. l. llanensis*, both with 2N = 70, FN = 68-69, and no biarmed autosomes. In contrast, *G. lutescens lutescens* from central and western Nebraska differs greatly in the number of biarmed autosomes (2N = 72, FN = 86-98, 16-28 biarmed autosomes; Hart, 1978), with some populations showing polymorphism. This includes populations previously placed in two other subspecies that are no longer considered valid, *G. l. hylaeus* and *G. l. vinaceus*, in addition to *lutescens*.

The contact zone between *G. attwateri* and *G. breviceps* has been described in detail by Honeycutt and Schmidly (1979) and Tucker and Schmidly (1981). They found that *G. breviceps sagittalis* has a diploid number of 74 and fundamental number of 72-74, and *G. attwateri* has a diploid number of 70, and fundamental number of 72-74.

This brief summary shows that diploid number varies from 70 to 74, and with one exception, fundamental number varies from 68 to 74. The one aberrant karyotype within the group is that of *G. lutescens lutescens*, with a diploid number of 72, but a fundamental number of 86 to 98.

Timm *et al.* (1982) reported karyotypes from 24 *Geomys* from the vicinity of the contact zone between *G. bursarius* and *G. lutescens* near Oakdale, Antelope Co., Nebraska. Two *G. b. bursarius* from 2¼ mi. E Oakdale, Antelope Co. (which is four miles east of the center of the contact zone), had karyotypes identical to those reported by Hart (1978) for a single individual from 1 mi. W Tilden, Antelope Co. (2N = 70, FN = 68, with no biarmed autosomes, and a large metacentric X). Eight gophers karyotyped from 1⅞ mi. W Oakdale and areas to the west of that point had karyotypes identical to those described by Hart (1978) for *G. l. lutescens* from Chadron, Dawes Co., and 4 mi. S Neligh, Antelope Co. (2N = 72, FN = 86-98, 16-28 biarmed autosomes).

Twelve gophers from the area between the parental types (from ⅝ mi. W Oakdale to 1⅛ mi. W Oakdale) had fundamental numbers ranging from 75 to 95. Six individuals had fundamental numbers intermediate between the parental types (FN = 75 to 82), and one of these six had 2N = 71. Because of the high variability in FN in the parental population of *G. lutescens* (FN = 84-92), it is not possible to say whether the karyotypically intermediate individuals are F_1 hybrids or backcrosses. It is apparent that the change from the *G. bursarius* to *G. lutescens* cytotype takes

place over a distance of about one-half mile (Timm *et al.*, 1982).

EVIDENCE FROM PARASITES

As part of our study of relationships of *Geomys* in the Great Plains, lice (Mallophaga: Trichodectidae) of the genus *Geomydoecus* were obtained from all species and subspecies of *Geomys* that were recognized previously, for use as an additional taxonomic character. A revision of the *Geomydoecus* on the *Geomys bursarius* complex resulted in redescription of the four previously recognized species of lice, description of four additional species, and refinement of our knowledge of the distribution of lice on pocket gopher taxa (Timm, 1979; Timm and Price, 1980; Timm, 1983). Taxa of *Geomydoecus* are distinguished primarily on the morphology of the genitalia of both males and females, but also on differences in chaetotaxy, size, and the distinctive antennal scape of the males. These characters exhibited little intrapopulational variation, but varied considerably geographically. No individual or population of *Geomys* was found to be parasitized by more than one species of *Geomydoecus*, and in general, a single species of louse was found throughout the range of a taxon or group of taxa of pocket gophers.

The *Geomydoecus* on the *Geomys bursarius* complex cluster into two main groupings that Timm and Price (1980) termed the "northern group" and the "southern group." The "northern group" is composed of two complexes of species, the "*geomydis*" complex and the "*oklahomensis*" complex; the "southern group" is composed of three species (see Fig. 17).

Northern Group.—*Geomydoecus geomydis* is found only on two subspecies of pocket gophers, *Geomys bursarius bursarius* and *G. b. wisconsinensis.* It was found on all individuals examined from throughout the range of the two subspecies, except for those pocket gophers in the vicinity of St. Louis, Missouri, previously referred to as *G. b. missouriensis.* The second member of the "*geomydis*" complex, *Geomydoecus illinoensis,* is restricted to one geographically isolated subspecies of pocket gopher, *G. b. illinoensis.* Although definitely a member of the "*geomydis*" complex, this louse is quite distinctive in several metric features and so clusters separately from *G. geomydis* (Timm and Price, 1980).

The second complex in the northern group includes three species, *Geomydoecus oklahomensis, G. nebrathkensis,* and *G. spickai,* and was termed the "*oklahomensis*" complex. *Geomydoecus oklahomensis* was found on the following

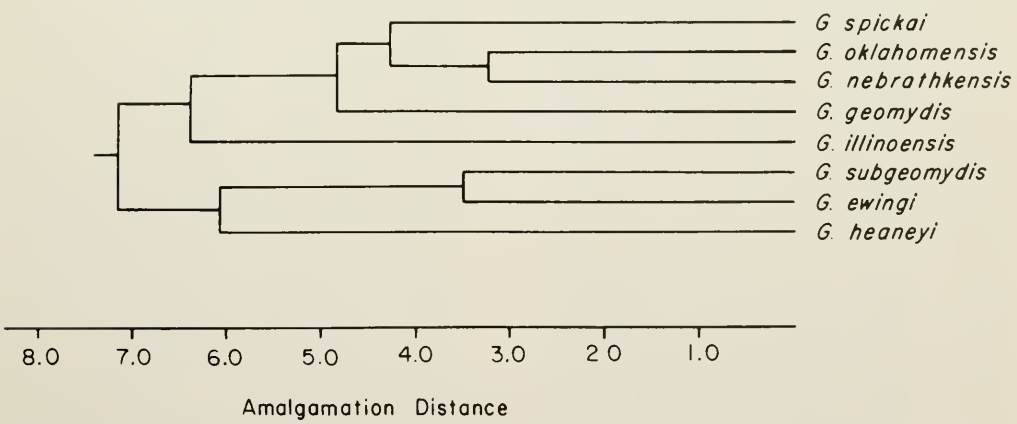

FIG. 17.—Phenogram of morphological similarity of eight species of lice *(Geomydoecus)* that parasitize *Geomys* based on cluster analysis of species means. (From Timm and Price, 1980. Reprinted with permission of the Journal of Medical Entomology).

pocket gopher taxa: *G. l. knoxjonesi, G. l. lutescens,* and *G. l. major.* The pocket gophers from southwestern Nebraska, western Kansas, Oklahoma, and Texas, and eastern Colorado and New Mexico all are parasitized by this species of *Geomydoecus.* Although this louse was the most variable and the most widely distributed of the eight species found on the *G. bursarius* complex, there was no evidence that any of the populations warranted classification as a distinct taxon. The lice on two previously recognized subspecies of pocket gophers, *industrius* and *jugossicularis,* appeared to be one uniform population.

Geomydoecus nebrathkensis is found only on populations of *G. l. lutescens* found north of the Platte River in northern Nebraska, northeastern Colorado, eastern Wyoming, and southern South Dakota and not on other populations of this gopher subspecies. The presence of *G. nebrathkensis* north of the Platte River may represent a speciation event for the lice which is not reflected in morphological differentiation of the hosts.

Geomydoecus spickai is found only on the pocket gophers in the vicinity of St. Louis, Missouri, the population that previously was considered a distinct subspecies, *G. b. missouriensis.* The presence of this species of louse on pocket gophers that are now considered *Geomys b. bursarius* on morphological and karyotypic grounds represents a discordance between relationships suggested by the parasite data and that suggested by other kinds of data. At present we know nothing about what lice may have occurred on pocket gophers in southern and central Missouri, and we must tentatively conclude that the presence of *G. spickai* on this one population of *Geomys bursarius* represents a dispersal event not parallel to host speciation.

Southern Group.—*Geomydoecus heaneyi* is found on only two subspecies of pocket gophers, *llanensis* and *texensis. G. heaneyi* is a very distinctive louse and its presence on both *llanensis* and *texensis* suggests that they are most closely related to each other.

Geomydoecus subgeomydis is found on two species of pocket gophers, *Geomys attwateri* (in part) and *G. breviceps sagittalis. Geomydoecus ewingi* is found on two species of pocket gophers, *G. attwateri* (in part), and *G. breviceps.* The presence of *G. ewingi* on *G. b. breviceps* and *G. b. sagittalis* supports the conclusion of Honeycutt and Schmidly (1979) that *breviceps* is most closely related to *sagittalis.*

The boundary that Honeycutt and Schmidly (1979) drew between *Geomys attwateri* and *G. breviceps sagittalis* is in close agreement with the boundary between the two species of lice, *Geomydoecus subgeomydis* and *G. ewingi;* however, the match is not perfect (Timm and Price, 1980). In general, *G. ewingi* is found on the eastern species, *G. breviceps,* and *G. subgeomydis* is found on the western species, *G. attwateri.* However, along the Brazos River some populations of *Geomys* that Honeycutt and Schmidly (1979) referred to the eastern species, *G. breviceps,* were parasitized by the western louse, *G. subgeomydis.* Also, there is a population of the eastern louse, *G. ewingi,* in Atascosa, Bexar, Goliad, and Wilson counties, Texas, that is separated by a population of *G. subgeomydis* from the main body of *G. ewingi.* An analysis of the lice showed that there was no justification for splitting the two separated populations of *G. ewingi* into two or more taxa (Timm and Price, 1980). These discrepancies suggest that our understanding of the systematics and host relationships of the *Geomys* and *Geomydoecus* of southeastern Texas warrants further investigation.

RELATIONSHIPS OF THE EXTANT SPECIES OF *GEOMYS*

Relationships of the living species of *Geomys* have been considered in detail only by Merriam (1895) and Russell (1968); the phylogenetic trees they proposed are shown in Fig. 18. The pre-

ceding pages contain a body of data that may be used to test these previously proposed phylogenies, and may also be used if necessary to construct a new phylogenetic tree that is more in concordance with available data. Because we have detailed data from only three of the extant species, some of our conclusions must be tentative. However, some definitive statements can be made.

In his revision of the Recent Geomyidae, Merriam (1895) considered *Zygogeomys trichops* to represent a species similar to the ancestor of *Geomys*. Within *Geomys*, he considered the *G. breviceps* group (including *G. arenarius, G. breviceps, G. personatus*, and *G. tropicalis*) to be the most primitive, with *G. pinetis, G. lutescens*, and *G. bursarius* representing progressively more derived species (Fig. 18A). Russell's (1968) study of relationships of genera was based on fossil as well as Recent material. Like Merriam, he considered *Zygogeomys trichops* to be close to the ancestry of *Geomys* (Fig. 18B). However, he considered *G. pinetis* to be the most primitive living species, and placed *G. breviceps* (in synonymy with *G. bursarius*) among the most derived forms. He placed *G. personatus* and *G. arenarius*, respectively, as progressively more derived species in a lineage leading to *G. bursarius* (including *G. breviceps* and *G. lutescens*).

The first conclusion that we may draw is that Russell (1968) was incorrect in considering *G. breviceps* and *G. lutescens* to be synonyms of *G. bursarius*. This might have had little effect on his concept of relationships if the three species form a monophyletic clade, but it should be recognized that he lumped them because he followed Villa-R. and Hall (1947), rather than because of critical examination of evidence. Merriam (1895) was correct in separating the three species.

Our phenogram of cranial similarity (Fig. 10) suggests a closer relationship between *G. lutescens* and *G. breviceps* than between either of these and *G. bursarius*. This is not relevant to Russell's phylogeny (Fig. 18B), because he considered all three to be conspecific. It does not support Merriam's phylogeny (Fig. 18A), since he indicated a closer relationship between *G. lutescens* and *G. bursarius* than between either and *G. breviceps*.

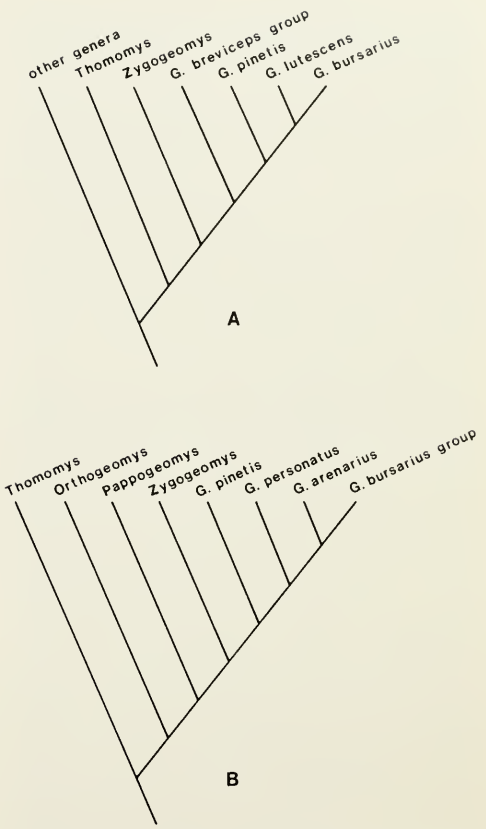

FIG. 18.—Hypothesized phylogenetic trees of geomyids suggested by: A. Merriam (1895: 24), and B. Russell (1968).

Morphology of the bacula appears to be of little help in discerning relationships, since with one exception the difference between taxa appears to be well correlated with size, which cannot necessarily be assumed to indicate relationship. The one exception is *G. lutescens lutescens*, whose relatively stout baculum may be considered a derived character.

Because the homologies of individual chromosomes are unknown in most of

the species of *Geomys* (i.e., little banding has been carried out), there is little definitive information content in the data available. The most aberrant karyotype among the taxa considered in this study is that of *G. lutescens lutescens,* which has a large number of biarmed chromosomes. It is most probable that this is a derived condition, with the possession of all or nearly all acrocentric chromosomes representing the primitive condition in this group.

The phylogeny of the ectoparasitic lice *(Geomydoecus)* found on *Geomys* (Timm and Price, 1980; Fig. 17) suggests a close relationship between *G. bursarius* and *G. lutescens,* with *G. breviceps* being the sister-group, and so is in accordance with Merriam's tree (Fig. 18A). Relationship of lice on other species of *Geomys* are not explicitly expressed (Price and Emerson, 1971).

Our cladistic analysis of seven cranial features using the Wagner Tree method (Fig. 13) is in better concordance with the phylogeny proposed by Merriam (1895) than Russell's (1968), but is not identical to either. Our analysis supports Merriam's suggestion that *G. bursarius* and *G. lutescens* are highly derived sister-groups. The analysis supports Russell's suggestion that *G. pinetis* is an early off-shoot of the *Geomys* stock, and that *G. personatus* is close to the ancestry of *G. lutescens* and *G. bursarius.*

We conclude from this discussion that the weight of evidence does not support either Merriam's (1895) or Russell's (1968) hypothesized phylogeny of *Geomys.* A tree that fits the data should have the following features. First, *Geomys pinetis* should be shown as an early offshoot of the main stock, as indicated by its generally primitive set of characters. Second, *G. personatus* should be shown as similar to *G. breviceps,* and both as potential sister-species to the *G. lutescens–G. bursarius* clade. Third, *G. lutescens* should be shown as being intermediate between *G. breviceps* and *G. bursarius.* Fig. 19 is our estimate of the phylogeny that best represents these features.

One significant feature that emerges from this study and is emphasized in our consideration of phylogenetic relationships is that parapatric and allopatric populations of pocket gophers often develop discrete, unique cranial characters before they become genetically independent of one another, that is, before they attain species level (i.e., the subspecies of *G. bursarius* and *G. lutescens*). This suggests that analyses of taxonomic relationships near the species level of differentiation must give substantial attention to evidence of intergradation between taxa. Any analysis that deals only with qualitative characters, and does not investigate geographic variation, is likely to err in overestimating the number of species present in any given group. A second important feature that is evident is that limited hybridization, such as appears to exist between *G. bursarius* and *G. lutescens,* and between *G. lutescens* and *G. breviceps,* is not a useful indicator of relationship, since such hybridization is not confined to sister-species.

BIOGEOGRAPHIC INTERPRETATIONS

Although our knowledge of the Pleistocene flora and fauna of the Great Plains has advanced greatly in recent years (see, for example, Dort and Jones, 1970), current paleobotanical data are insufficient to infer the extent of prairie vegetation patches that might have been

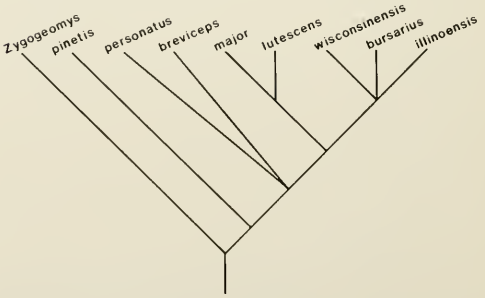

FIG. 19.—Hypothesized phylogenetic tree of selected extant species of *Geomys* based on results of this study.

critical to differentiation of pocket gophers. For this reason, the following discussion is general in scope, and deals with major glacial advances and floristic changes. We present this as a plausible hypothesis which may be tested with more detailed knowledge of the Pleistocene history of the Great Plains and the gophers themselves.

The *Geomys bursarius* and *G. pinetis* complexes originated no later than the late Irvingtonian, as offshoots from either *G. garbanii* or *G. tobinensis* (Kurtén and Anderson, 1980). The earliest records of the *G. bursarius* complex are from the Yarmouthian of Ellsworth County, Kansas (Hibbard *et al.,* 1978). We suggest that the ancestors of the two major clades in the *G. bursarius* complex, the *breviceps* group (including *attwateri, arenarius, personatus,* and *tropicalis*), and the *bursarius* group (*bursarius* and *lutescens*), split during the Kansan glaciation, with the *breviceps* group speciating during some uncertain later time. The split between *G. bursarius* and *G. lutescens* probably occurred during the Illinoian glaciation when glacial advances, and probably forest expansion, were at a maximum. The subsequent interglacial, the Sangamonian, was most likely a period of some expansion for the prairie (or savannah) flora and fauna, and *Geomys* were recorded from Kansas, Nebraska, Oklahoma, and Texas during this period (Hibbard, 1970; Russell, 1968). We suggest that during the Sangamonian, approximately 200,000 years BP, *Geomys* spread to most regions it currently occupies. During the subsequent stage of glaciation, the Wisconsinan, many of the populations of pocket gophers were isolated as forest and glaciers advanced; most must have become extinct as their habitat was reduced. Continental glaciers gradually moved to cover much of the area now occupied by *Geomys* in the northern portions of its range. Probably all of Minnesota (Wright and Ruhe, 1965) and eastern North and South Dakota (Lemke *et al.,* 1965) were covered by ice. Only a small portion of southwestern Wisconsin was ice-free (Frye *et al.,* 1965), but the presence of *Geomys* cf. *bursarius* (Hay, 1923: 343), *Thomomys talpoides,* and other small mammals shows that a region of forest parkland remained throughout the Wisconsinan (Rasmussen, 1971).

Illinois and Indiana were nearly completely covered by glaciers during the Illinoian glaciation, but were ice-free during the Sangamonian, and were only partly glaciated during the Wisconsinan (Frey *et al.,* 1965). *G. bursarius* persisted in this region, as indicated by the discovery of *G. bursarius* of Wisconsinan age in central Indiana, southern Illinois, Kentucky, and central Tennessee (Parmalee and Klippel, 1981). The presence of *Geomys* and *Microtus ochrogaster* show that forest parkland existed south of the glacier front in Indiana and Illinois (Parmalee *et al.,* 1978). The Wisconsinan faunas reported by Parmalee (op. cit.) and Guilday *et al.* (1971) from this area are much like that occurring today in the vicinity of Minneapolis, Minnesota, in mixed deciduous and coniferous forest with patches of tall-grass prairie where *G. bursarius* is abundant. The analyses of relationships discussed above do not support the suggestion by Parmalee and Klippel (1981) that the now-extinct Kentucky and Tennessee populations of *G. bursarius* gave rise to *G. pinetis,* since these are only distantly related.

Although the Des Moines Lobe covered much of the central part of the current range of *G. bursarius,* many areas in southeastern Iowa, southeastern Nebraska, and eastern Kansas were not glaciated. The presence of grass, sagebrush, and ragweed pollen in late Wisconsinan lake sediments in northeastern Kansas indicates the persistence of prairie islands in conferous forest in this region (Wright, 1970). A specimen of late Pleistocene age from Pottawatomie County, Kansas (KUVP 25299), that appears to us to be *G. bursarius* indicates that this species occurred in the area. It is possible that *G. bursarius* occurred

farther south in the central plains during this period (i.e., outside of its present range), but we have no evidence of this.

Geomys lutescens may have been absent from northern Nebraska and adjacent areas during the Wisconsinan stage because of the coniferous forest widespread there; certainly they were absent at the close of the Wisconsinan because the shifting sands of the Nebraska Sandhills (Wright, 1970) could not have supported them. *Geomys lutescens* probably persisted throughout the Wisconsinan in western Kansas where coniferous parkland was widespread (Stewart, 1979); fossil *Geomys* (initially referred to *lutescens,* but in recent years referred to *bursarius*) are known from several faunas in Meade County, Kansas (Russell, 1968; Davis, 1975), and from Rooks County (McMullen, 1978). The current level of divergence between *G. l. lutescens* and *G. l. major* suggests that theirs is secondary intergradation, but we know of no certain isolating factor. Perhaps a band of continuous forest separated populations of *G. l. lutescens* in Kansas from populations of *G. l. major* in Texas; detailed studies of Wisconsinan gophers from these areas and of their associated faunas may yield sufficient information to evaluate this hypothesis.

While Wisconsinan climatic changes in the central and northern Great Plains probably resulted in restrictions in the distribution of *Geomys,* the cooler, wetter conditions may have allowed expansion in Texas, Oklahoma, New Mexico, and northern Mexico. The southern species of *Geomys* (*G. arenarius, G. personatus,* and *G. tropicalis*) may have originated via allopatric speciation prior to the Wisconsinan, perhaps during the hotter, drier conditions of the Sangamonian. The hypothesis that they originated via parapatric (= "stasipatric" of some authors) speciation during the Wisconsinan is equally possible, although equally untested.

At the close of the Pleistocene, massive changes took place in the flora of central North America, marked by the extinction of many mammals, and great changes in the distributions of most others (Guilday, 1967; Martin and Neuner, 1978). Pocket gophers of the genus *Geomys* probably expanded their ranges in most areas because the climatic changes taking place favored the spread of their habitat, the prairies. *Geomys lutescens* expanded into relatively dry portions of the central Great Plains in western Nebraska and adjacent states, and *Geomys bursarius* expanded into moist portions of the plains in eastern Nebraska, Iowa, and Minnesota. At least two of the isolated populations survived the Wisconsinan; these are now represented by *G. b. illinoensis* and *G. b. wisconsinensis.* In the southern Great Plains, gopher distributions undoubtedly became restricted as aridity increased, leaving relict populations of *G. arenarius, G. attwateri, G. breviceps, G. personatus,* and *G. tropicalis* scattered across the southern plains. Subsequent climatic events undoubtedly modified the distributions of the gophers, but the major features of *Geomys* distribution we see today were probably determined by about 8,000 BP.

The location of the current zone of contact between *G. bursarius* and *G. lutescens* in Kansas was investigated by plotting all known localities of occurrence on the map of potential natural vegetation prepared by Küchler (1974). The distribution of the two species is defined with remarkable accuracy by the line marking the western boundary of prairie with significant forest islands. In the southern part of the state the line lies well to the east of the border of tall-grass prairie, and in the northern part of the state, especially near the Nebraska border, the line lies to the west of the limit of tall-grass prairie, but in all cases the line defines the distribution of the gophers. We plotted all known localities of *Geomys* in Nebraska on the map of natural vegetation prepared by Kaul (1975). All records of

G. lutescens lie in mixed, sandhills, or short-grass prairie. Most records of *G. bursarius* are from areas having tall-grass prairie, but a few records from Adams and Knox counties are from the transition zone between mixed and tall-grass prairie. We have drawn our estimate of the boundary line between the two groups (Fig. 1) based on these observatons.

SUMMARY

Three species of pocket gophers of the genus *Geomys* exist in the Great Plains north of Texas. The northernmost of these, *G. bursarius,* consists of the widespread, variable nominate subspecies and two more restricted, less variable subspecies (*G. b. illinoensis* and *G. b. wisconsinensis*). The second species, from the central plains, *G. lutescens,* has two subspecies within the study area (*G. l. lutescens* and *G. l. major*), and one or more extralimital subspecies. The third species, *G. breviceps,* is represented in the southern plains (in Oklahoma) by *G. b. sagittalis*, and by several subspecies outside of our study area. All species are distinguishable on the basis of cranial morphology, karyology, and ectoparasite fauna, and show minor differences in bacula. All specimens previously thought to be intergrades between the three species were reexamined and found to be clearly assignable to one species or the other, with no evidence of intergradation. Hybridization between *G. bursarius* and *G. lutescens* occurs only at a single locality in Nebraska, and introgression there is inconsequential. Hybridization between *G. lutescens* and *G. breviceps* probably occurs in several places in east-central Oklahoma, but the hybrid zones are narrow, and gene flow appears to be restricted. Variation within all species is mostly clinal; non-clinal variation is thought to be due to the late-Pleistocene history of the gophers. Analysis of cranial and other characters indicates that *G. bursarius* and *G. lutescens* are recently derived from a stock similar to *G. breviceps* and *G. personatus. Geomys pinetis* had the most primitive features of the species considered, and was probably separated from the others at an early date.

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ADDENDUM

Several important papers have appeared since this manuscript was accepted for publication. In the first, Honeycutt and Williams (1982) used starch-gel electrophoresis to examine intergeneric relationships within the subfamily Geomyinae. Both a cladistic analysis and a cluster analysis using similarity coefficients indicated that *Geomys* is one of the earliest lateral branches in the subfamily, but is generally most similar to *Zygogeomys,* also an early lateral branch. They suggested that *Orthogeomys* is the sister-group of *Zygogeomys.*

Williams (1982) described the phalli of geomyids in detail, including those of the taxa referred to here as *Geomys arenarius, G. attwateri, G. breviceps sagittalis, G. lutescens lutescens, G. lutescens major, G. personatus,* and *G. pinetis.* A cluster analysis of a set of phallus measurements suggested that *G. breviceps* is the sister-group of *G. lutescens;* that *G. arenarius* is the sister-group to that lineage; that *G. attwateri* is the sister-group to *G. "lutescens" llanensis* and *texensis;* and that *G. pinetis* and *G. personatus* lie outside of this group. Because no *G. bursarius* as defined here were included, no direct comparison to our phylogeny of the *G. bursarius* group is possible. We suggest that a phenetic analysis that restricts the effect of size and a cladistic analysis of these data, with a sample of *G. bursarius* added, would comprise a suitable test of our proposed phylogeny.

Finally, Hafner (1982) used electrophoretic and immunological data to examine relationships of the Geomyoidea. His data support the monophyly of the Geomyidae and Geomyinae. Unlike the results of Honeycutt and Williams (1982), he found evidence for considering *Pappogeomys* to be the sister-group of *Geomys,* but in general found his data inadequate for consideration of generic or subgeneric relationships.

In summary, although these studies add substantially to the perspective of this paper, they do not affect our conclusions regarding the relationships of species in the *Geomys bursarius* species group.

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APPENDIX I

All specimens from the zone of contact between *Geomys bursarius* and *G. lutescens* near Oakdale, Antelope County, Nebraska, utilized in the preceding analyses are listed here.

Geomys bursarius

Specimens examined. — Nebraska: *Antelope Co.:* 2⅒ mi. S Oakdale (1 SM); W edge Oakdale (8 SM); ½ mi. W Oak-

dale (3 SM); 2/10 mi. S, 7/10 mi. W Oakdale (6 KU); 2/10 mi. S, 6/10 mi. W Oakdale (5 KU).

Geomys bursarius × *Geomys lutescens*

Specimens examined. — NEBRASKA: *Antelope Co.:* 2/10 mi. S, 7/10 mi. W Oakdale (1 KU); 2/10 mi. S, 6/10 mi. W Oakdale (1 KU); 1/10 mi. N, 6/10 mi. W Oakdale (3 KU); 2/10 mi. N, 8/10 mi. W Oakdale (2 KU); 1 mi. W Oakdale (16 KU, 6 SM); (vicinity of) Oakdale (1 USNM).

Geomys lutescens

Specimens examined. — NEBRASKA: *Antelope Co.:* 2/10 mi. S, 1 mi. W Oakdale (1 KU); 2/10 mi. N, 1 mi. W Oakdale (5 KU); 1/10 mi. N, 1 1/10 mi. W Oakdale (1 KU); 1 1/10 mi. W Oakdale (1 KU); 1/10 mi. N, 1 2/10 mi. W Oakdale (2 KU); 1/10 mi. S, 1 2/10 mi. W Oakdale (3 KU); 1 1/10 mi. W Oakdale (9 KU); 1½ mi. W Oakdale (1 SM); 2 mi. W Oakdale (1 SM); (vicinity of) Oakdale (1 USNM).

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